FORAGING ECOLOGY AND SOCIALITY OF MUSKOXEN IN NORTHWESTERN ALASKA

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FORAGING ECOLOGY AND SOCIALITY

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ABSTRACT

I investigated sociality and winter foraging ecology of muskoxen (*Ovibos moschatus*) in Cape Krusenstern National Monument, northwestern Alaska. The nutritional value of moss (*Hylocomium splendens*, *Tomenthypnum nitens*) for muskoxen was evaluated by incubating moss in rumen-fistulated muskoxen and simulating post-ruminal digestion by incubation in acid-pepsin. Moss was indigestible in muskoxen and gained mass and nitrogen in the rumen. Consequently, high moss consumption during winter may result in net loss of nitrogen from a muskoxen's system. Local and regional differences in moss use by muskoxen and caribou or reindeer (*Rangifer tarandus*) were investigated in northwestern Alaska in relation to indicators of winter range quality. On muskox winter ranges, increases in fecal moss indicated decreased graminoid cover, harder snow, increased moss cover, and greater animal densities. Higher mobility of caribou than muskoxen during winter limits use of their feces to reflect local forage selection, but fecal moss may indicate caribou winter range quality on a larger, regional scale. Increasing proportions of moss in muskoxen feces may alert wildlife managers to shifts in forage availability due to changing snow conditions.

Roles of male and female muskoxen in coordinating group movements were investigated during the snow-free season. Adult females led most activity initiations, foraging-bout movements, and spontaneous group movements. Rutting males actively manipulated female-led movements through herding and blocking. Leaders incurred no costs in terms of lost foraging time. Habitat use by muskoxen shifted from upland habitats in early summer towards lowland sedge meadows during rut. Muskox group

sizes decreased from winter to summer to rut. Muskoxen foraging efficiency decreased with group size in spatially unlimited but not in spatially limited habitats. Adult males contributed least to group cohesion, and their presence may contribute to group fission during rut. A conceptual model is presented which discusses how habitat, foraging, social behavior, and predation threat contribute to group sizes, fission and fusion of muskox groups. Results from this study indicate that winter ranges used by muskoxen in Cape Krusenstern may be limiting, which suggests that numbers of muskoxen in this area will likely remain small. Therefore, hunting quotas should be low and limited to males only.

TABLE OF CONTENTS

Page

Signature Page i

Title Page ii

Abstract iii

Table of Contents v

List of Figures x

List of Tables xii

List of Appendices xiii

Acknowledgments xiv

General Introduction 1

References 5

CHAPTER 1

Nutritional value of moss for arctic ruminants: a test with muskoxen 8

1.1 Abstract 8

1.2 Introduction 9

1.3 Study Area 11

1.4 Methods 12

1.41 Study Animals and Forages 12

1.42 Ruminal Degradation of Forages 13

1.43 Acid-Pepsin Digestion 14

Page

1.44 Chemical Analyses 15

1.45 Statistical Analyses 15

1.5 Results 16

1.51 Ruminal Degradation of Forages 16

1.52 Acid-Pepsin Digestion 17

1.53 Ultrastructure of Mosses and Hay 18

1.6 Discussion 18

1.61 Ruminal Degradation of Forages 19

1.62 Post-Ruminal Digestion 21

1.7 Management Implications 22

1.8 Acknowledgments 23

1.9 Literature Cited 23

CHAPTER 2

Fecal moss as an indicator of wintering area quality for arctic ungulates 36

2.1 Abstract 36

2.2 Introduction 37

2.3 Study Areas 40

2.31 Cape Krusenstern 40

2.32 Seward Peninsula 41

2.4 Methods 42

Page

2.41 Spatial Scales of Investigation....42
2.42 Cape Krusenstern....43
2.43 Seward Peninsula....47
2.44 Data Treatment and Statistical Analyses....47
2.5 Results....48
2.51 Local and regional differences in fecal moss....48
2.52 Forage availability....49
2.53 Forage accessibility....49
2.54 Location....50
2.6 Discussion....50
2.61 Local and regional differences in fecal moss....51
2.62 Forage availability....51
2.63 Forage accessibility....51
2.64 Location....55
2.65 Circumpolar comparison of moss use by caribou and muskoxen....56
2.7 Management Implications....58
2.8 Acknowledgments....59
2.9 Literature Cited....59

Page

CHAPTER 3

Leadership in mixed-sex groups of muskoxen during the snow-free season . 77

3.1 Abstract 77

3.2 Introduction 78

3.3 Study Area 81

3.4 Methods 82

3.41 Data treatment and statistical analyses 84

3.5 Results 85

3.51 Population demographics and observational statistics 85

3.52 Initiators of group activity 86

3.53 Leaders of foraging-bout movements 87

3.54 Leaders of spontaneous group movements 87

3.55 Leadership by individuals 88

3.56 Cost of leadership 88

3.6 Discussion 88

3.7 Acknowledgments 93

3.8 References 94

CHAPTER 4

Fission and fusion in muskox groups 108

4.1 Abstract 108

Page

4.2 Introduction 109

4.3 Study Area 112

4.4 Methods 113

4.41 Data treatment and statistical analyses 116

4.5 Results 118

4.51 Abundance, demographics and group size 118

4.52 Habitat use 118

4.53 Foraging efficiency 119

4.54 Sociality 120

4.6 Discussion 121

4.61 Conceptual model: effect of habitat 122

4.62 Conceptual model: effect of foraging 123

4.63 Conceptual model: effect of sociality 125

4.64 Conceptual model: effect of predation 127

4.65 Decisions by individuals based on physiological state 128

4.66 Management implications 129

4.7 Acknowledgments 130

4.8 References 130

General Conclusions 147

References 152

LIST OF FIGURES

Page

Figure 1.1: Ruminal action of three forages and a synthetic sponge 33

Figure 1.2: Potential post-ruminal release of dry matter (DM), nitrogen (N), and ash after in vitro acid-pepsin incubation 34

Figure 1.3: Micrographs of ground and dried samples of hay and Fairbanks moss (F-moss) before exposure to the rumen 35

Figure 2.1: Study area in Cape Krusenstern National Monument 68

Figure 2.2: Relationship between fecal moss and percent cover 69

Figure 2.3: Relationships between fecal moss and muskox density (A) and terrain ruggedness (B) 70

Figure 2.4: Profiles and topographic maps of three muskox wintering areas 71

Figure 2.5: Percent moss in summer and winter feces 72

Figure 3.1: Location of Cape Krusenstern National Monument 103

Figure 3.2: Group leadership in muskoxen in three behavioural contexts 104

Figure 3.3: Distribution of leadership 105

Figure 3.4: Active time spent feeding by non-leaders and leaders 106

Figure 3.5: Three examples how a herd bull manipulated movements 107

Figure 4.1: Location of Cape Krusenstern National Monument 141

Figure 4.2: Use of spatially bounded and unbounded habitat types 142

Figure 4.3: Foraging efficiency (percent of active animals feeding) 143

Page

Figure 4.4: Relationship between habitat use (a) and individual spacing (b) versus group size 144

Figure 4.5: Nearest-neighbor distances across sex-age classes 145

Figure 4.6: Conceptual model of factors influencing fission and fusion 146

LIST OF TABLES

Page

Table 1.1: Published estimates of moss digestibility in *Rangifer tarandus* ssp 31

Table 1.2: Composition of hay and moss used for ruminal incubations 32

Table 3.1: Sexual differences between successful and unsuccessful initiations . 101

Table 3.2: Outcome of spontaneous group movements 102

Table 4.1: Seasonal changes in sex-age composition and size of mixed-sex muskox groups..... 139

Table 4.2: Percent vegetation cover at six major habitat types 140

LIST OF APPENDICES

Page

Appendix 2.1: Discernible plant fragments (100 views per slide) 73

Appendix 2.2: Parameters associated with muskox and caribou wintering areas in Cape Krusenstern National Monument 74

Appendix 2.3: Parameters associated with muskox wintering areas on the northern Seward Peninsula 75

Appendix 2.4: Parameters associated with feeding sites of mixed groups of reindeer and caribou 76

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GENERAL INTRODUCTION

Muskoxen (*Ovibos moschatus*) have been present in Alaska from the Pleistocene (Harington 1970) until the mid-1800s, when the last indigenous Alaskan muskoxen were shot on the North Slope. In an effort to establish viable populations in Alaska, 30 young muskoxen from Greenland were released on Nunivak Island in the 1930s. In later decades, four additional populations were established in northern and western Alaska: Nelson Island, the Seward Peninsula, Cape Thomsen, and The Arctic National Wildlife Refuge. At Cape Thomsen in northwestern Alaska, muskoxen were released in 1970 and 1977 (Grauvogel 1984). The population subsequently expanded to include Cape Krusenstern National Monument to the south and is currently stable at approximately 300-400 animals (Dau 2005).

Since the introduction of muskoxen to Alaska, regional differences in population growth have intrigued wildlife managers. For example, the population on the Seward Peninsula initially grew slowly, increased about 14% annually during the 1990s to over 2000 animals, and finally slowed its growth in recent years (Persons 2005). In contrast, the muskox population in northwestern Alaska between Cape Krusenstern and Point Hope never grew only about 8% annually until 1997 and has since stabilized at approximately 300-400 animals (Dau 2005).

One of the initial motivations for the introduction of muskoxen was to provide rural people with another large animal for subsistence hunting. U.S National Park Service biologists responsible for managing the muskox population in Cape Krusenstern National Monument north of Kotzebue were anticipating a muskox hunt in that area, but

they also were concerned that they needed more information on the biology of the Cape Krusenstern muskox population in order to be able to set hunting quotas and predict how a hunt might affect the population. Some of the questions that concern managers are these: Why has the Cape Thomsen population, which includes muskoxen in Cape Krusenstern, not grown as fast as that on the Seward Peninsula? Is further population growth likely, or are muskoxen in Cape Krusenstern facing habitat or winter range restrictions that limit carrying capacity in that area? What are the roles of different sex and age classes in muskox society? Should a hunt include females or target bulls only? How stable are individual groups over time, and will the shooting of mature individuals of either sex disrupt group structure or result in reduced reproductive success? Will hunting displace animals from critical habitat components?

My first experience in Cape Krusenstern National Monument was a one-week survey of two muskox winter ranges, which I conducted for the National Park Service in July 1999. During that trip, I made two observations upon which I later based a part of my PhD research: First, winter ranges in Cape Krusenstern were unlike those I had previously studied on the northern Seward Peninsula (Ihl 1999). The wind-blown hilltops where muskoxen spent much of their winters were smaller, the slopes steeper, and the vegetation sparser. Most hilltops were partially barren, with much bare ground and a patchy carpet of mountain avens (*Dryas* spp), interspersed with sedges (*Carex* spp) and a few mossy areas. Second, fecal samples I collected at the two winter ranges differed greatly in the amount of moss and graminoids they contained. Although graminoids are known to be the primary winter forage of muskoxen (Klein 1992), the

role of mosses in the diets of Arctic ungulates has generated various interpretations (White 1983). For example, in caribou and reindeer (*Rangifer tarandus* ssp), moss is generally considered to be a poorly digestible forage that is incidentally ingested when the animals search for lichens, their primary winter forage, and increases in the diet when lichens are rare (Parker 1978, Staaland et al. 1993). It follows that winter ranges, where muskoxen forage for up to eight months out of the year, and the diets they obtain there, are an important factor in the biology of muskoxen in Cape Krusenstern.

The social organization of muskoxen has fascinated me ever since I first began studying the species. In particular, after many field hours of watching muskox herds travel, forage, and mingle with other groups, I was curious how muskoxen coordinate group movements. Whether certain individuals or sex-age classes take a leadership role during group movements is also an important question for managers of muskox populations when considering which sexes and age classes should be hunted. Several recent theoretical studies demonstrate, using mathematical models, that coordinated movements of even very large groups are possible without the need for group leaders (Conradt and Roper 2003, Couzin et al. 2005). Nevertheless, researchers who have studied social mammals in the field have observed that individuals or particular sex and age classes, especially adult females, are often leaders or initiators of group movements (Boinski 1993, Prins 1996).

In my research, I address two factors which are of key importance in helping managers understand muskoxen in Cape Krusenstern: sociality and foraging, with particular emphasis on the foraging situation on winter ranges. Chapters 1 and 2

examine the winter foraging ecology of muskoxen, whereas chapters 3 and 4 are concerned with social behavior and group movements of muskoxen during summer.

The first chapter examines the nutritional value of moss for muskoxen. Although estimates of digestibility for mosses exist for reindeer and caribou, it was previously unknown whether muskoxen digested moss differently. This study (Ihl and Barboza 2007) presents the first digestibility estimate for mosses in muskoxen and concludes that moss is not only indigestible in muskoxen, but that eating moss may place animals in a negative energy and protein balance.

The second chapter builds upon the findings of the first by interpreting the ecological significance of moss use by Arctic ungulates and raises the question: if moss is a low quality forage, what does moss intake by caribou and muskoxen tell managers about the properties of wintering areas? This chapter examines how the percentage of moss in feces of caribou and muskoxen relates to quality of wintering areas for both species. It concludes that for muskoxen, increasing moss can indicate decreased graminoid availability, harder snow, and higher animal densities on winter ranges on a small local scale. For caribou populations, fecal moss can reveal quality differences in winter ranges at a larger, regional scale.

To examine how muskoxen make group-level decisions, the third chapter focuses on the role of leaders during three types of group movements: slow foraging movements, spontaneous non-foraging movements, and initiation of group activity. Females are leaders of most group movements, although rutting bulls actively manipulate movements of females.

Finally, the fourth chapter integrates observations on group movements, composition and group foraging decisions with findings from the other three chapters and the literature to build a conceptual model of the factors driving fission and fusion in muskox groups in different seasons.

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CHAPTER 1

NUTRITIONAL VALUE OF MOSS FOR ARCTIC RUMINANTS: A TEST WITH MUSKOXEN[1]

1.1 ABSTRACT:

Although moss is commonly found in the feces of arctic herbivores, we do not know the digestible value of this forage for ruminants. We compared grass hay (*Bromus* spp.) with moss (*Hylocomium splendens*, *Tomenthypnum nitens*) from two locations in Alaska: Cape Krusenstern National Monument and Fairbanks. We evaluated forages by digestion in ruminally fistulated muskoxen (*Ovibos moschatus*) by suspending forages in polyester bags before and after the rumen was acclimated with moss for 15 consecutive days. Ruminal degradation was not affected by acclimation to moss. Hay lost dry matter during 48 hr of ruminal incubation (-49%), whereas moss gained dry matter (+44 to 57%). Incubated moss gained nitrogen (+435 to 680%), as well as fiber (+18%), and one moss gained ash (+ 121%). Mass gained by moss in the rumen was probably due to the combined effect of microbial colonization and adsorption of fibrous particles onto the sponge-like matrix. We evaluated post-ruminal degradation of forages by incubation in acid-pepsin. Ruminally incubated mosses lost little nitrogen in acid-pepsin even though ruminally incubated hay lost 23% nitrogen on acid digestion. Consumption of moss during winter may be a net cost of selecting plants within moss

[1] Ihl, C., and P.S. Barboza. 2007. Nutritional value of moss for Arctic ruminants: a test with muskoxen. Journal of Wildlife Management 71(3):752-758.

communities when lichens and graminoids are scarce. Moss in feces may therefore indicate low availability of favored foods for muskoxen and other arctic ruminants that are confined to small winter ranges. Increasing concentrations of moss in the feces and thus the diet of muskoxen may alert wildlife managers to shifts in winter range quality or forage access due to changing snow conditions.

Key words: acid digestion, Arctic ungulates, dry matter disappearance, moss, muskoxen, *Ovibos moschatus*, winter diet.

1.2 INTRODUCTION

Mosses are among the most common plants at high latitudes and are consumed by many herbivores (Batzli and Cole 1979, Staaland et al. 1983, Prop and Vulnik 1992, Barten et al. 2001). Among Arctic ungulates, dietary moss content varies seasonally and with both region and latitude. Generally, caribou (*Rangifer tarandus*) (Parker 1978, Post and Klein 1999) and muskoxen (*Ovibos moschatus*) (Parker 1978, Klein and Bay 1990) eat more moss in winter than in summer.

In *Rangifer*, there may be an inverse relationship between lichen availability and moss intake. Increased moss intake by reindeer and caribou has been observed on overgrazed, lichen-depleted winter ranges (Staaland et al. 1993). Lichen-poor ranges in the high arctic (>75°N) are also associated with high moss consumption for Svalbard reindeer (23-65% in feces; Staaland et al. 1993) and Peary caribou (21-86% in feces; Parker 1978, 13-58% in feces; Thomas and Edmonds 1983). Similarly, for muskox

populations in Canada and Greenland, ruminal and fecal moss concentrations increase with latitude (Canada: < 1%-22% in rumen from 73-80°N; Wilkinson et al. 1976, Parker 1978, Greenland: < 2%-27% in feces from 71-82°N; Thing et al. 1987, Klein and Bay 1990). Exceptions to this latitudinal trend are caribou and muskox populations in Alaska, where moss concentrations in ruminal digesta and feces are consistently high during winter (caribou: 13-48% in feces; Biddlecomb 1991, Saperstein 1993, Post and Klein 1999, muskoxen: 19-41% in feces; Biddlecomb 1991, Wilson 1992, Ihl and Klein 2001).

The importance of moss as a source of nutrients for herbivores is not well established. Parker (1978) noted an inverse relationship between percent marrow fat of Peary caribou and rumen moss contents, suggesting that high moss ingestion is indicative of nutritionally stressed animals. Animals may incidentally eat moss with preferred forages such as lichen and graminoids because those plants grow among the moss layer. Consequently, moss intakes may increase as preferred forages decrease in biomass (Parker 1978, White 1983). However, White (1983) and Staaland et al. (1988) hypothesized that moss may be a source of minerals such as sodium, calcium, and phosphorus for reindeer, as has been shown for lemmings (Batzli et al. 1980).

The digestibility of moss varies widely from 1-48 % in *Rangifer*, and few values are available for other species of herbivores (Table 1.1). Moss is composed of fibrous cell walls that require microbial fermentation in the rumen or the large intestine. The presence of large amounts of moss in the rumen of Svalbard reindeer does not apparently inhibit fermentation rates when the availability of alternate forages such as

lichen and sedge are low (Staaland et al. 1988). Microbial fermentations change with season and with substrate in muskoxen (Peltier et al. 2003, Barboza et al. 2004); therefore, ruminal microbes may require time to adapt to novel substrates such as moss (Dehority 2003). This observation is supported by measures of digestibility in vitro using ruminal inocula from reindeer with different exposure to wild forages (Thomas and Kroeger 1980, Trudell et al. 1980).

Muskoxen in northwest Alaska appear to rely on moss during winter since fecal pellets collected on winter ranges contain up to 75% moss (C. Ihl, unpublished data). Consequently, we tested the hypothesis that moss is digestible forage and has nutritional value for muskoxen in winter. Ruminal degradation is a reliable indicator of forage quality in muskoxen because the reticulorumen accounts for 79% of dry matter disappearance along the digestive tract in winter (Barboza et al. 2006). No previous estimates of moss digestibility exist for muskoxen. Digestibility estimates for mosses in muskoxen will help interpret range and forage quality of wild muskoxen, as well as the significance of dietary differences between muskoxen on different winter ranges.

1.3 STUDY AREA

We conducted our study on captive muskoxen at the R.G. White Large Animal Research Station at the University of Alaska Fairbanks, USA (65°N 146°W).
We collected moss in two sites: Cape Krusenstern National Monument (67°N 163°W) on the Chuckchi Sea coast in northwestern Alaska, and in boreal forest near Fairbanks, Alaska (65°N 146°W). Vegetation throughout Cape Krusenstern is Arctic coastal

tundra. There are several hill groups up to 613 m in elevation, which muskoxen use as wintering areas. Hilltops are generally covered with *Dryas* heath and lower slopes with hummock tundra. *Hylocomium splendens, Tomenthypnum nitens* and other mosses used by muskoxen grow in clumps among *Dryas* and cover the tops of hummocks (Ihl, unpublished data). At our Fairbanks moss collection site, *Hylocomium splendens*, other feather mosses and *Sphagnum* spp. grow as an extensive carpet in black spruce (*Picea mariana*) muskeg forests.

1.4 METHODS

1.41 Study Animals and Forages

We tested forage digestion in 4 adult castrated males with rumen fistulas that were established 5 years before this study (protocol #04-02 of the Institutional Animal Care and Use Committee). We held animals in outdoor enclosures of approximately 1ha with ad libitum grass hay (*Bromus* spp.) and water or snow. We fed a pelleted mineral supplement (M Ration; Alaska Pet and Garden, Rombach et al. 2002) at $35g \cdot kg^{-1}$ body mass each week. We did not feed supplements during measures of in situ degradation to exclude any effects on ruminal fermentation. We weighed animals daily throughout the study (± 0.1 kg) to monitor body condition.

We compared nutrient composition and digestibility of moss with grass hay consumed in captivity. We sub sampled hay from bales fed to study animals during the experiments. We collected a total of 108 kg of frozen moss from two regions in Alaska. We attempted to mimic the foraging behavior of wild muskoxen by sampling bite-size

clumps of the loose upper layer of live moss every 1-3 m. We collected the first batch of moss (K-moss) in April 2004 from winter ranges of muskoxen in Cape Krusenstern National Monument. K-moss was mainly composed of *Hylocomium splendens* and *Tomenthypnum nitens,* but it contained small amounts of several other moss species, as well as fragments of lichen, sedge, and evergreen shrubs. We collected a second batch of moss (F-moss) near Fairbanks (65°N 146°W) in October 2004. F-moss was more homogenous in composition than K-moss and consisted mainly of *Hylocomium splendens*. We stored mosses frozen for experiments in January and February 2005.

1.42 Ruminal Degradation of Forages

We measured in situ degradation before and after acclimatization of the rumen to each batch of moss. We used a crossover design with two periods in which we acclimatized all animals to each moss for 15 days. We inoculated 2 animals daily with K-moss and 2 animals with F-moss in each period. We partially thawed and broke up moss clumps by hand to mimic mastication. Daily inoculations of moss were approximately 250 g dry mass, which we inserted directly into the rumen fistula of each animal. We measured in situ degradation for up to 96 hr for each moss with hay as a control.

We prepared moss and hay for in situ measures by drying to constant mass at 50 C. We ground dried forages through a 2 mm mesh in a Wiley Mill. We estimated fractional disappearance of dry matter (DM) by modifying an in situ method previously used by other researchers (e.g., Van Keuren and Heinemann 1962, Person et al. 1980,

Barboza et al. 2006). We sealed samples of 2-3 g of forage in tared, permeable polyester bags (5 x 10 cm; 50 μm pore size; Ankom Technology, Macedon NY) and suspended them in the rumen. We attached 10 bags to a weighted polypropylene rope, which we attached to the fistula plug for subsequent retrieval. We used at least two replicates of each forage in each animal at each removal time. We added empty bags to each chain to control for changes in the mass of the bags. We removed bags at 24, 48, and 96 hr, rinsed them under running water to remove material attached to the outside, and dried them at 50 C to constant weight. We expressed the residual DM as a proportion of the original dry mass.

We used synthetic sponge as a reference for in situ measures after acclimation to moss. We assumed that mass changes in the sponge were due to adsorption and absorption of dry mass and microbes and that microbial degradation of the synthetic material was negligible. We dried and ground sponge in the same manner as forages.

1.43 Acid-Pepsin Digestion

We tested the potential for post-ruminal digestion of forages with a modification of the in vitro procedure by Tilley and Terry (1963). We incubated forages in 2 gL^{-1} of porcine pepsin (Mallinckrodt, Baker Paris KY Cat # 2629-57) with 0.2 M phosphate buffer at pH 2.5. We then combined approximately 6 ml of this solution with 0.5-1.0 g of dried and ground forage in a vial. We incubated and gently agitated vials in a water bath at 38 C for 24 hr. We washed precipitates twice in distilled water after centrifugation for 10 min at 12,300 x g and then dried them to constant mass at 50 C to

determine the change in DM during incubation. We tested forages before and after incubation in the rumen: hay 0, 48 hr; moss 0, 48, and 96 hr. We compared acid degradations of forages fed to muskoxen with two controls: alfalfa hay (*Medicago sativa*) and bovine casein (Fisher, Leicestershire, UK).

1.44 Chemical Analyses

We analyzed forages and ruminal residues for neutral detergent fiber (NDF), total nitrogen (N), and ash content following the procedures of Peltier et al. (2003). We analyzed acid residues only for DM, N, and ash.

We described changes in forage structure during incubation in the rumen by preparing images with an Environmental Scanning Electron Microscope (Electroscan, model E2020). We selected ground and dried samples of hay, K-moss, and F-moss before exposure to the rumen and after 48 hr in the rumen. We suspended a small amount of each sample on a piece of adhesive tape and mounted it under a microscope for viewing.

1.45 Statistical Analyses

We report arithmetic means and standard errors of each group. We used repeated-measures ANOVA to test the effect of acclimatization of the rumen on moss digestibility and to test whether there was a time effect on the digestibility of hay controls between weeks. We expressed changes in mass of ruminally incubated samples or acid pepsin incubations as g/original g and compared them with the pre-incubation

standard of 1 by using a one-sample t-test because we expected a reduction in mass. We used repeated-measures ANOVA to test for differences in ruminal residues between 24 and 48 hr for hay and at 48 and 96 hr for moss. We used Bonferroni adjustments for multiple comparisons in all t-tests within each forage class. We conducted all analyses with SYSTAT 10.2.

1.5 RESULTS

All four animals maintained their body weights (285 ± 1 kg) during the study. Hay contained less 13 and 12% less NDF than F-moss and K-moss, respectively. F-moss contained 59% and K-moss 53% less N than hay. Hay contained 68% less ash than F-moss, but only 22 % less ash than K-moss. Variances on all forage analyses were < 5% (Table 1.2).

1.51 Ruminal Degradation of Forages

Hay lost 50 ± 3% DM mostly in the first 24 hr of ruminal incubation ($P = 0.001$, $t = -17.33$, df = 3). Maximal degradation of hay at 48 hr was 52% before acclimation to moss and 44 to 59% after the acclimation period. Ruminal incubation of hay apparently removed 50 ± 3% of NDF ($P < 0.001$, $t = -16.46$, df = 3) and 32 ± 4% of ash ($P = 0.004$, $t = -7.77$, df = 3). Hay residues apparently gained as much N as was lost because residual N was 94 ± 6% of the original N in the forage ($P = 0.39$, $t = -1$, df = 3; Fig. 1.1).

Acclimatization of the rumen to moss for 15 days had no effect on DM changes of either moss or hay (repeated measures ANOVA, $P = 0.32$, $F = 1.49$, df = 6). Through 96 hr of incubation in the rumen, F moss gained 57% DM ($P = 0.021$, $t = 6.61$, df = 3) and K-moss gained 44% DM ($P = 0\ 042$, $t = 5.12$, df = 3) (Fig. 1.1). Similar to mosses, synthetic sponges gained DM (142%) when incubated in the rumen for 96hr ($P = 0.032$, $t = 4.94$, df = 3; Fig. 1.1).

Ruminal incubation added large amounts of N to both mosses. Gains of N to the original moss were 455 to 680% for F-moss ($P < 0.001$, $t = 22.58$, df = 3) and 383 to 435% for K-moss ($P = 0.002$, $t = 12.32$, df = 3) after 48 hr in the rumen. Gains of NDF in the rumen were similar between mosses (+18%) after 48hr, but were not significant (F-moss: $P = 0.05$, $t = 4.171$, df = 3; K-moss: $P = 0.294$, $t = 1.946$, df = 3). Ash uptake differed between mosses (Fig. 1.1). The moss with the lowest initial ash content (K-moss) gained up to 121% of the original ash ($P = 0.005$, $t = 9.24$, df = 3), whereas F-moss did not significantly gain ash ($P = 1.0$, $t = 0.079$, df = 3).

1.52 Acid-Pepsin Digestion

Alfalfa and casein contained 3.0 and 15.0% N, respectively. In vitro incubation with acid-pepsin was sufficient to remove both DM and N from alfalfa (27 ± 0% DM, 62 ± 0% N) and from casein (38 ± 4% DM, 38 ± 4% N) (Fig 1.2). Hay that was not previously incubated in the rumen lost 15 ± 1% of DM and 41 ± 1% of N in acid digests. Moss that was not previously incubated in the rumen did not lose DM during acid digestion (Fig 1.2). Acid digestion removed less than 8% of DM from ruminal

residues of hay and moss. Ruminal residues of hay lost 23 ± 0.8% N in acid digests, whereas only 7-14% of N was lost from moss residues. Ash losses from forages were variable in acid digests and were not significantly different from zero for all except alfalfa (43%) and one residue of F-moss (27%) (for all significant results $P < 0.05$, $t < -6.3$, df = 2; Fig. 1.2).

1.53 Ultrastructure of Mosses and Hay

Micrographs of hay and moss before and after incubation in the rumen revealed that ruminal incubation of hay produced a similar ultrastructure at the resolution of 200-300 μm. In contrast, moss surfaces appeared laden with particles after ruminal incubation (Fig. 1.3).

1.6 DISCUSSION

Our results indicate that moss is poorly digestible in muskoxen, and its consumption may even result in a net loss of nutrients from the animal. We therefore reject our hypothesis that moss is a digestible forage for muskoxen. Our study animals showed no interest in eating mosses voluntarily, which confirms the low herbivore preference for mosses observed by other researchers (Batzli and Cole 1979, White and Trudell 1980, Staaland et al. 1988). This low preference is consistent with the low protein content and high fiber concentration of moss (Table 1.2; Boertje 1981, Staaland et al. 1988).

1.61 Ruminal Degradation of Forages

Moss is probably not completely indigestible in muskoxen because other herbivores can degrade DM in moss (Table 1.1). Any dry matter disappearance in the rumen is, however, masked by uptake of material. Ruminal uptake of dry mass is likely a result of the open structure of moss, which entraps small particles in a similar fashion to sponge (Fig 1.1). Dry mass gains in the rumen are further enhanced by adsorption of particles onto the surface of moss. Micrographs show that mosses accumulate fibrous particles from other forages such as graminoids (Fig. 1.3).

Ionic attractions probably play a role in surface adsorption of different mosses depending upon their mineral composition. For example, metals bind to peat moss (*Sphagnum* spp.) by displacing protons or existing metals from anionic sites (Crist et al. 1996). Ash is a general indicator of mineral content in forages that is primarily due to Ca, K, P, and Mg (Van Soest 1994). Staaland et al. (1988) suggested that moss might have some nutritional value for reindeer and caribou by providing minerals. Specifically, moss may provide Ca for *Rangifer* on a lichen diet or increase availability of P in a diet of graminoids (Staaland et al. 1988). Nevertheless, in our study, ruminal uptake of mineral ash was inversely proportional to the initial ash content of the moss (Fig 1.1). Consequently, the amount and availability of minerals in mosses will vary widely depending upon the binding capacity of the moss matrix and the interactions between ions within the moss, other forages, and the ruminal fluid. Release of minerals in the rumen varies between forages (Emanuelle and Staples 1990) and with the

composition of the rumen (Staaland et al. 1980). More research is necessary to look at the relationship between mineral content and binding capacities of mosses in different areas of the arctic (sensu Ohlson and Staaland 2001).

Why have other studies of moss digestion reported net DM disappearance in vitro, in situ, and in vivo? The answer may lie partly in the applied methodology. Most moss digestion studies have used in vitro methods that strain rumen liquor to remove particles (Person et al. 1980, Thomas et al. 1984). This may have prevented particle uptake during measures of digestion in vitro. Furthermore, ruminal digesta of reindeer and caribou are generally less fibrous than those of muskoxen, causing moss to take up fewer particles. This is especially true of captive animals: reindeer and caribou are typically fed a concentrated pelleted feed (Trudell et al. 1980, Staaland et al. 1988), while muskoxen are maintained mainly on hay (Adamczewski et al. 1994, Barboza et al. 2004). The highest published value for moss digestibility is 48%, as determined by a feeding trial on Svalbard reindeer (Staaland et al. 1988). Those authors note, however, that this value is questionable because it is based on a very low intake by only one animal. Small herbivores such as microtine rodents (Batzli and Cole 1979) do digest moss, albeit at low rates. Moss use by microtines may differ from that of ruminants because the rodents may be able to select more digestible parts of the plant and thus achieve higher overall digestibilities.

1.62 Post-Ruminal Digestion

Microbial colonization of moss probably contributes some DM to the residue, but mainly increases the low N content in the forage. Bacterial N may be recovered from ruminal residues passing to the abomasum and the small intestine, where most N is absorbed in muskoxen (Barboza et al. 2006). The amounts of N removed from mosses during acid digestion in vitro were much smaller than initial N gains during ruminal incubation. K-moss gained 409% N in the rumen and lost only 10% during in vitro acid digestion, whereas F-moss gained 568% in the rumen and lost only 14% in acid. Moss leaving the abomasum would therefore represent a net gain of 400 and 550% N in K- and F-moss, respectively. Thus, moss ingestion may result in a net loss of N to the animal because it is unlikely that all absorbed N in moss is removed and reabsorbed in the small intestine and the hind gut. In contrast, net loss of N from hay was 23%, which constitutes a net N gain for the animal. This pattern of in vitro digestion is consistent with the pattern of digestion along the digestive tract of muskoxen fed grass hay (Barboza et al. 2006).

Large grazers such as muskoxen have the ruminal capacity to retain slowly digested forages (Hofmann 2000, Knott et al. 2004). Prolonged retention of moss would favor the attachment of microbes and any subsequent digestion of that fibrous matrix. The degradability of mosses is, however, very low because the matrix is resistant to acid-pepsin degradation. A slowly digested matrix is not likely to provide sufficient energy for replication of even a small subpopulation of microbes. Exposure to moss for

15 days did not alter in situ degradation rates for muskoxen and is consistent with the poor profitability of moss for microbes. Acclimation to moss is either very slow or negligible, especially in winter when food intakes of muskoxen and ruminal bacterial numbers are at their lowest (Peltier et al. 2003, Barboza et al. 2004).

The cost of consuming moss may be acceptable to the ruminant as long as moss intakes remain low and incidental to the ingestion of more digestible forages, such as graminoids and lichens. Increased appearance of moss in feces can mean either that more moss has been ingested, or that fewer other forages have been eaten. Because we do not know DM intake of wild ungulates on winter ranges, we do not know which of these scenarios applies. In either case, an increased proportion of moss in the feces or ruminal digesta would indicate low availability of preferred forages. Presumably, when other forages on winter ranges have been depleted, ungulates bite further into the moss layer to reach graminoid stem bases or lichens interspersed with moss.

1.7 MANAGEMENT IMPLICATIONS

Because moss is poorly digestible and can remove N from the animal, ungulates may be in a negative energy and nutrient balance at times of high moss consumption. Increases in moss use over time could point to progressive overgrazing of winter ranges or increasingly limited access to preferred forages due to changing snow and climatic conditions. Because of their low digestibility, mosses are likely overrepresented in the feces of most herbivores. Nonetheless, relative comparisons of fecal moss content among herbivore populations may point to temporal and spatial differences in diets as

well as general range quality. This knowledge can aid managers in formulating management objectives such as reintroduction sites, dispersal corridors, and harvest levels for muskox populations.

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TABLE 1.1: Published estimates of moss digestibility in *Rangifer tarandus* ssp.

Rangifer tarandus ssp.	Moss species	Method	Digestibility estimate [%]
tarandus	*Aulacomnium turgidum*	IVDMD 48hr	1-16[h]
	Polytrichium alpinum	IVDMD 48hr	6-18[h]
	Pleurozium schreberi	bag DMD 48hr	16-25[c]
	Hylocomium splendens	IVDMD	19[i]
	Sphagnum magellanicum	IVDMD	6[i]
sibiricus	*Hylocomium splendens*	bag DMD 48hr	5.9[b]
	Hylocomium splendens	IVDMD 48hr	19[b]
	Polytrichium juniperinum	bag DMD 48hr	13.2[b]
	Polytrichium juniperinum	IVDMD 48hr	13.6[b]
	Sphagnum magellanicum	bag DMD 48hr	3.4[b]
	Sphagnum magellanicum	IVDMD 48hr	4.4[b]
platyrhynchus	*Aulacomnium turgidum*	IVDMD 48hr	1-16[h]
	Polytrichium alpinum	IVDMD 48hr	3-12[h]
	Pleurozium scherberi	feeding trial	48.1[d]
groenlandicus	*Polytrichium piliferum*	IVDMD 63hr	15[f]
	Ptilidium ciliare	IVDMD 63hr	24[f]
	Sphagnum spp.	IVDMD 63hr	19[f]
	various	IVDMD 60hr	7-28[g]
pearyi	various	IVDMD 60hr	3-35[e]
granti	not specified	IVDMD	7[a]

References: [a] Boertje 1981, [b] Person et al. 1980, [c] Staaland and Garmo 1987, [d] Staaland et al. 1988, [e] Thomas and Kroeger 1980, [f] Thomas and Kroeger 1981, [g] Thomas et al. 1984, [h] Trudell et al. 1980, [i] White et al. 1975.

TABLE 1.2: Composition of hay and moss used for ruminal incubations in muskoxen at the R.G. White Large Animal Research Station, Fairbanks, Alaska, Jan-Feb 2005.

Composition	Hay[c]	F-moss[d]	K-moss[e]
DM[a] g/100g wet weight	92.1	31.5	17.7
NDF[b] g/100g DM	66.5	76.3	76.0
Nitrogen g/100g DM	1.7	0.7	0.8
Carbon g/100g DM	45.1	40.4	46.9
Ash g/100g DM	6.3	19.6	8.1

[a] Dry Matter, [b] Neutral Detergent Fiber, [c] *Bromus* spp., [d] Fairbanks moss; *Hylocomium splendens*, [e] Krusenstern moss; mix of *Tomenthypnum nitens*, *Hylocomium splendens*, small amounts of other mosses and forages.

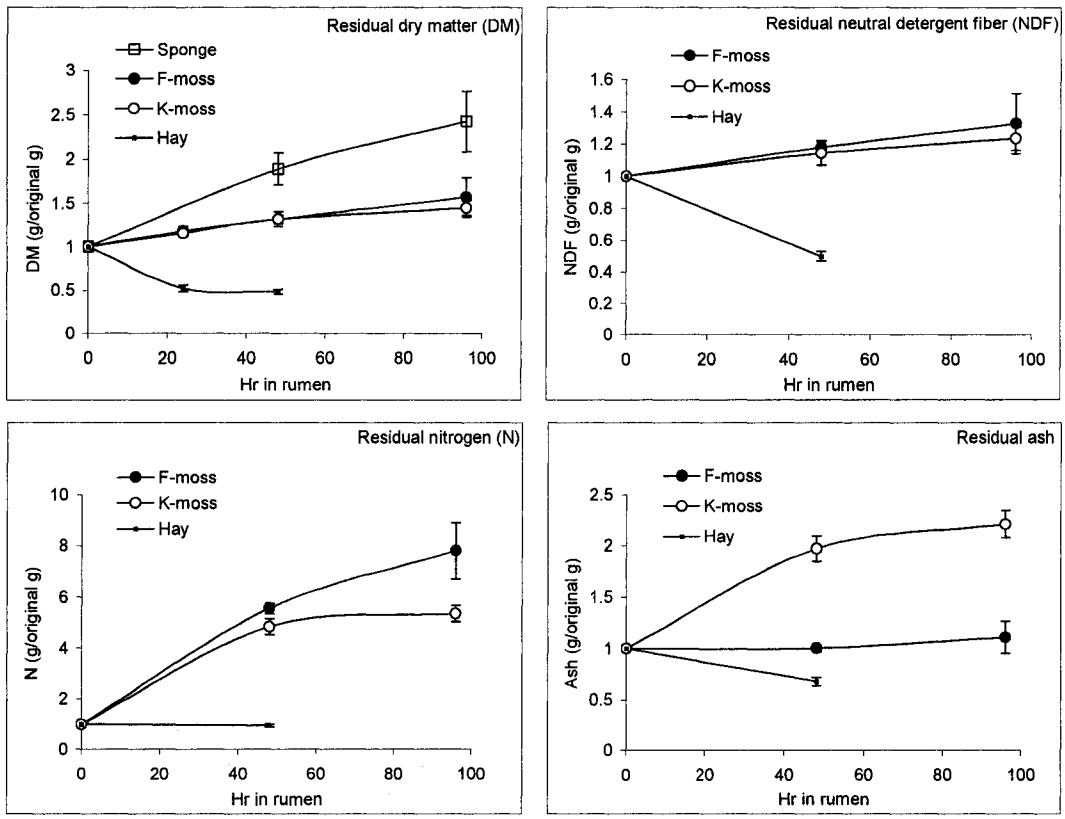

FIGURE 1.1: Ruminal action of three forages and a synthetic sponge control in four rumen-fistulated male muskoxen at the Robert G. White Large Animal Research Station, Fairbanks, Alaska, Jan-Feb 2005. Fractional weight change (g/original g) of dry matter (DM), neutral detergent fiber (NDF), nitrogen (N), and ash (mean ± SE).

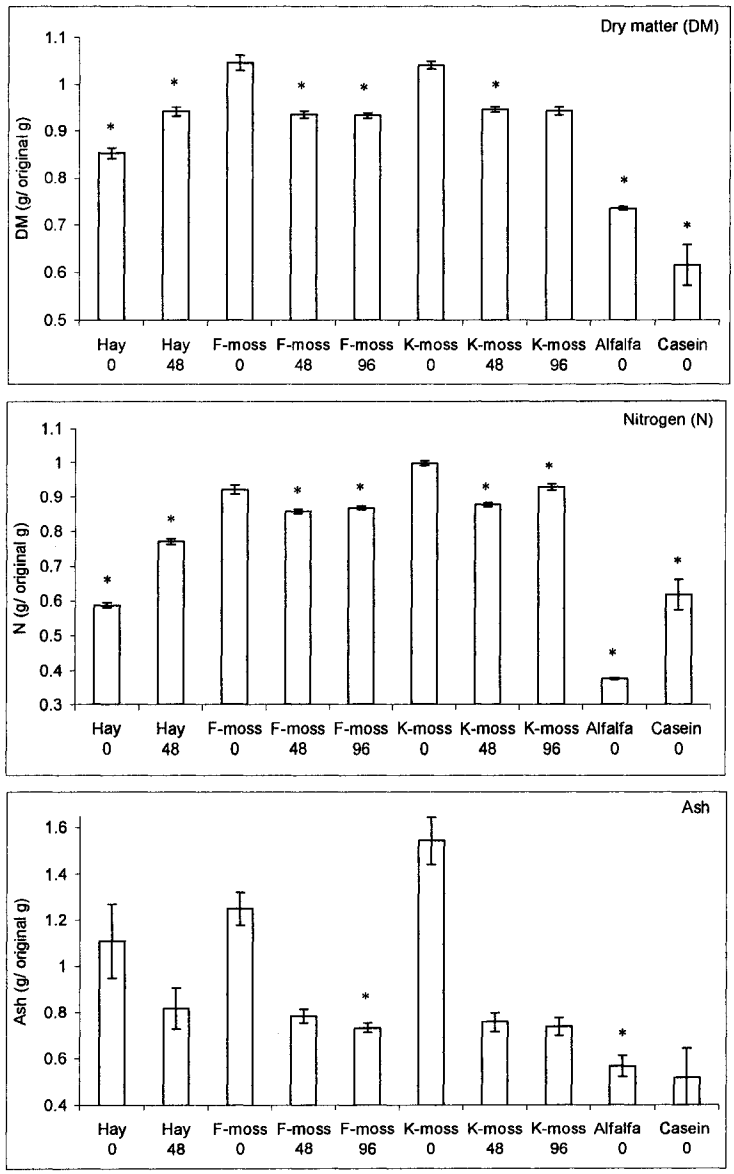

FIGURE 1.2: Potential post-ruminal release of dry matter (DM), nitrogen (N), and ash after in vitro acid-pepsin incubation for 24 hr (mean ± SE), in four rumen-fistulated male muskoxen at the Robert G. White Large Animal Research Station, Fairbanks, Alaska, Jan-Feb 2005. Numbers below columns indicate the duration of ruminal incubation prior to acid-pepsin digestion. Columns marked with * are significantly different from 1 ($P < 0.05$).

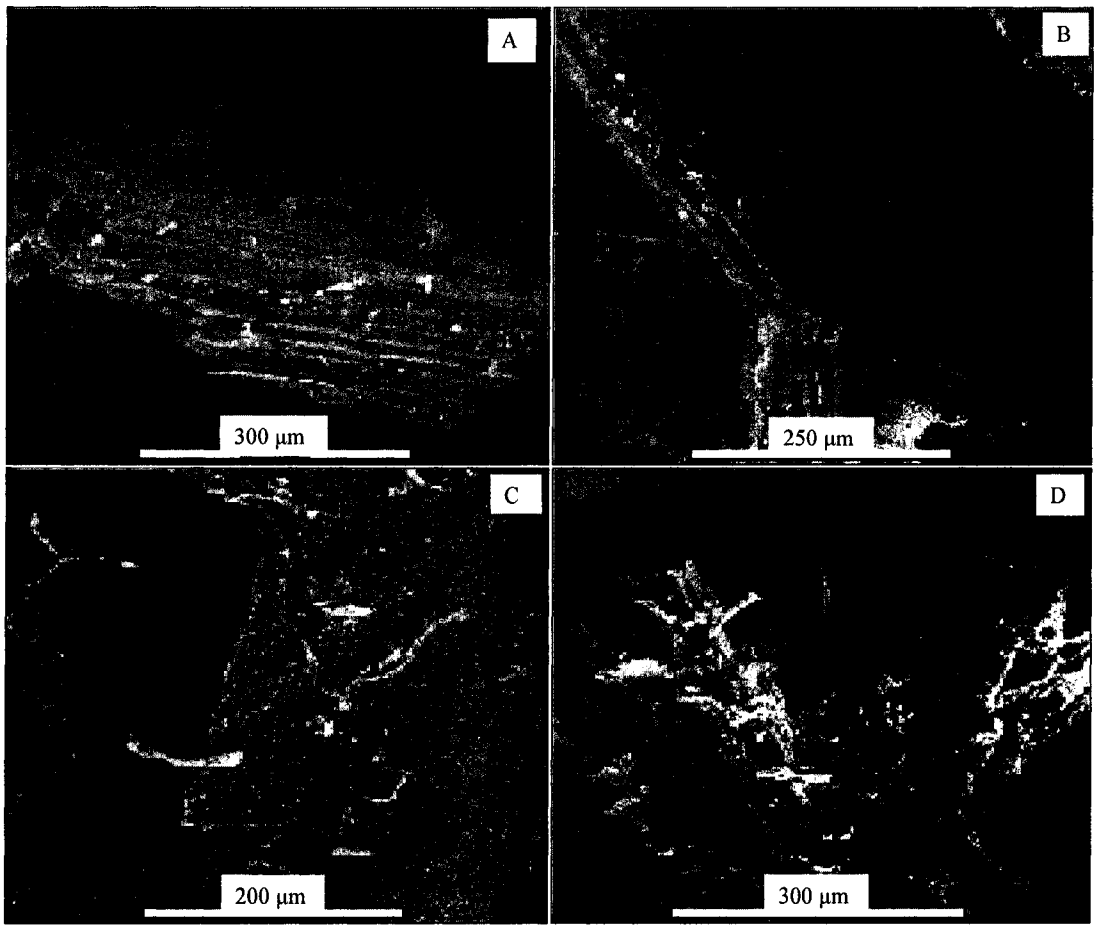

FIGURE 1.3: Micrographs of ground and dried samples of hay and Fairbanks moss (F-moss) before exposure to the rumen of a male muskox and after being suspended in the rumen for 48 hr, at the Robert G. White Large Animal Research Station, Fairbanks, Alaska, Jan-Feb 2005. A: hay pre-rumen, B: hay post-rumen, C: F-moss pre-rumen, D: F-moss post-rumen.

CHAPTER 2

FECAL MOSS AS AN INDICATOR OF WINTERING AREA QUALITY FOR ARCTIC UNGULATES[2]

2.1 ABSTRACT

I investigated local and regional differences in moss intake, as indicated by presence of moss in the feces of muskoxen (*Ovibos moschatus*) and caribou or reindeer (*Rangifer tarandus*) in northwestern Alaska, and related moss intake to forage availability, snow conditions, animal density, and terrain ruggedness on wintering areas. Percent moss in feces of muskoxen differed locally among individual wintering areas. Because of the large local variation in moss content of muskox feces, regional differences between the two study areas were difficult to resolve. Percent of moss in the feces of caribou did not differ between wintering areas within the same study area, but differed between study areas. On muskox wintering areas, fecal moss correlated negatively with graminoid cover and snow hardness and positively with moss cover and muskox density, but did not correlate with snow depth or terrain ruggedness. On caribou wintering areas, fecal moss correlated positively with moss availability, but not with lichen cover or snow depth or hardness. I conclude that fecal moss can be used as an indicator of wintering area quality for muskoxen. Caribou are more mobile than muskoxen in winter, and fecal samples may not be representative of the vegetative and

[2]Ihl, C. 2007. Fecal moss as an indicator of wintering area quality for arctic ungulates. Prepared for submission to Journal of Wildlife Management.

snow conditions at the wintering area where they were collected. Because muskox groups in Alaska are isolated from each other in winter, even groups wintering on neighboring hill tops may face different foraging availability and may therefore exhibit differences in productivity.

2.2 INTRODUCTION

Many researchers and managers of arctic ungulate populations have been occupied by questions of why muskoxen and caribou eat moss, and how to interpret varying amounts of moss in the diets of these animals (Parker 1978, White 1983, Staaland et al. 1993). Although digestibility estimates of moss for caribou and reindeer range from 0-48% (Trudell et al. 1980, Thomas et al. 1984, Staaland et al. 1988), researchers generally agree that mosses are poorly digested. A study on muskoxen (Ihl and Barboza 2007), using an *in situ* digestibility technique, indicated that moss is not only indigestible in muskoxen and yields little energy gain, but may also remove nitrogen from the animal because rumen microorganisms adhere to the moss matrix and are flushed from the digestive system. Moss intakes of muskoxen and caribou are highest in late winter, when access to forage is restricted by snow (Ihl and Klein 2001, Larter and Nagy 2001). Consequently, a high moss intake during late winter may place animals in a negative energy and protein balance when females are in their last trimester of pregnancy and preparing to lactate, and when fat and protein reserves are of critical importance (Barboza and Parker 2006). This raises the question whether moss use by muskoxen and caribou in late winter can provide clues to the quality of wintering areas.

What makes a high quality wintering area? Winter foraging by arctic ungulates is limited by snow hardness and depth (Adamczewski et al. 1988, Ihl and Klein 2001), availability of forages (Parker 1978, Staaland et al. 1993), and may be further influenced by topographical variation (Nellemann and Thomsen 1994, Nellemann 1996, Nellemann and Reynolds 1997). Muskoxen and caribou or reindeer in many arctic regions select feeding sites with shallower and softer snow than random areas (Biddlecomb 1991, Ihl and Klein 2001, Larter and Nagy 2001). Muskoxen are less well adapted to foraging through snow than caribou or reindeer (Klein 1992) and are typically restricted to spatially confined, windblown upland habitats in areas of high snow accumulation (Wilson 1992, Klein et al. 1993, Nellemann and Reynolds 1997, Ihl and Klein 2001). The cost of cratering may force muskoxen to use feeding craters more intensely, leading to a depletion of graminoids and an increased ingestion of mosses. Consequently, moss intake should be inversely related to availability of preferred, more nutritious forages: lichens for reindeer and caribou (Gaare 1997) and graminoids for muskoxen (Klein 1992).

Topography of wintering areas influences forage availability and snow distribution and the interaction between those factors (Nellemann and Thomsen 1994, Schaefer and Messier 1995*b*). Rugged terrain results in more varied vegetation and snow distribution (Nellemann and Fry 1995), which enables animals to find micro sites where they can forage more optimally in relation to forage quality, biomass, and snow chacteristics. Consequently, reindeer (Nellemann and Fry 1995) and muskoxen (Nellemann and Reynolds 1997) prefer to winter on ranges with greater terrain

ruggedness than surrounding areas. Rugged topography on wintering areas should increase access to preferred forages and reduce the need to foarge on mosses.

High densities of reindeer on wintering areas (Gaare 1997) depletes lichens, which in turn can lead to an increase of moss in the diet (Staaland et al. 1993). For muskoxen, animal density may be an even more significant issue, since muskoxen are spatially more confined on wintering areas than reindeer or caribou (Klein 1992). Graminoids may become depleted towards the end of winter, especially if large muskox groups forage on relatively small wintering areas.

The objective of this study is to examine local and regional differences in moss use by muskoxen and caribou in northwestern Alaska, and to relate moss use to three characteristics of wintering area quality: forage availability, forage accessibility, and physical range characteristics. I hypothesize that moss intake will be inversely related to availability of more preferred forages. Further, moss intake should increase when forage accessibility declines because of deep or wind-hardened snow. Lastly, ungulates should use more moss when animal density on wintering areas is high, whereas a high index of terrain ruggedness should allow animals to forage more effectively and should therefore lead to a decline in moss intake.

2.3 STUDY AREAS

2.31 Cape Krusenstern

Cape Krusenstern National Monument is a 2,670 km^2 area of coastal tundra along the Chukchi Sea in northwestern Alaska, USA (Fig. 2.1). Near the coast, narrow strips of sedge meadows line beach ridges and the edges of extensive lagoons. Further inland, several groups of hills (up to 613m elevation) are separated by wide expanses of gently rolling tussock tundra. Groups of muskoxen spend the autumn and early part of winter in low-lying sedge areas near the coast, but move to hilltops and ridges when snow accumulates in late winter. Hilltops and upper slopes are barren or covered with partially vegetated *Dryas* heath, and hummock tundra grows on lower slopes and hillsides. Strong winds from the northwest blow snow off exposed bluffs, ridges, and hilltops. During March and April 2001, these uplands were used by groups of muskoxen as wintering areas and were nearly free of snow. Occasionally, hilltops on muskox wintering areas were temporarily covered with newly fallen snow, but were blown free again within 1-2 days. Unlike muskoxen, caribou were not confined to hilltops during late winter 2001 but used habitats throughout the monument, including low-lying tussock tundra, hummock tundra on lower slopes, beach areas on the coast, and exposed, windblown uplands.

Winters in Cape Krusenstern National Monument are long (the time from first snow to green-up exceeds 7 months), and windstorms are frequent and severe. At Kotzebue (ca. 50 km south-east of Cape Krusenstern National Monument), annual

average temperature is -5.8 C and annual average precipitation is 22.5 cm, of which 12 cm falls between July and September. The lowest average minimum temperature is -24.4 C (February), and the highest average maximum temperature is 15.1 C in July.

After extirpation from Alaska in the late 1800s (Coady and Hinman 1984), muskoxen were introduced to northwestern Alaska in 1970 and 1977 when 36 and 34 muskoxen, respectively, were released near Cape Thompson in northwestern Alaska. The population grew at approximately 8% annually until 1997 and then stabilized (Dau 2005*a*). The population currently numbers 350-400 animals and has spread south to include Cape Krusenstern National Monument. An aerial survey in April 2002 identified 163 muskoxen in the monument.

The western Arctic caribou herd (*Rangifer tarandus*) numbered approximately 490,000 animals in July 2003 (Dau 2005*b*). During March and April 2001, caribou over-wintering in Cape Krusenstern National Monument formed groups typically numbering between 10-30 animals. Grizzly bears (*Ursus arctos*) are active in the area between late April and October, and wolves (*Canis lupus*) are present year-round. I observed two incidents of wolf predation on caribou during late winter, but the extent of predation by wolves and bears on muskoxen is unknown.

2.32 Seward Peninsula

The Seward Peninsula study area differs from Cape Krusenstern in that hilltops used by Arctic ungulates are generally lower in elevation, less windblown, and more vegetated. Most hilltops are covered with *Dryas* heath or hummock tundra (Swanson et

al. 1985). *Dryas* heath is generally 100% vegetated, not partially vegetated as in Cape Krusenstern. Hilltops on the Seward Peninsula were used by both muskoxen and mixed groups of reindeer and caribou during late winters of 1996 and 1997. Wolves and grizzly bears are present in the area. The study area on the northern Seward Peninsula is described in more detail in Ihl and Klein (2001).

2.4 METHODS

2.41 Spatial scales of investigation

I defined a crater as an area where a muskox, caribou, or reindeer had removed or disturbed the snow through pawing or pushing with the nose to reach the vegetation underneath. When no snow was present, I searched for signs of grazing such as cropped graminoids, lichen, or mosses and sampled vegetation over these sites in a similar manner as within craters. A feeding site was an area where groups of muskoxen, caribou, or reindeer had established clusters of several feeding craters or, in the absence of snow, where I had observed animals foraging. A wintering area was the area encompassing all feeding sites established by the same group of animals within a known time period. For muskoxen, this time period encompassed the whole study period, because muskox groups remained stationary or moved very little and, with one exception, remained on the same hilltops or ridgelines throughout the study period. For caribou and reindeer, the time interval used to define wintering areas included only 1-3

days, because caribou and reindeer groups moved large distances, which prevented me from relocating them over longer time periods.

2.42 Cape Krusenstern

Data collection included late winter (March 5 through May 6, 2001). In March 2001, the U.S. National Park Service, Western Arctic Parklands, conducted a survey of muskox groups in Cape Krusenstern National Monument. The survey located five mixed-sex muskox groups wintering on hill groups and one mixed-sex group on a beach area near the coast. In late winter, snow accumulation generally confines muskoxen to small wintering areas and groups move only short distances (Klein at al. 1993, Ihl and Klein 2001). This behavior made it easy to repeatedly re-locate each muskox group by snowmobile and on foot. I located caribou feeding sites by following fresh tracks on a snowmobile or by scanning with binoculars from hilltops until I sighted groups of foraging caribou. If I observed a group of caribou or muskoxen on a feeding site, I waited until the group had moved on before sampling that site. I sampled 17 muskox feeding sites and combined them to represent 6 muskox wintering areas.

At each muskox or caribou feeding site, I randomly selected 6 craters. At each crater, I visually estimated the percent cover of major vegetation classes (graminoids, mosses, lichens, shrubs, *Dryas* spp., and forbs) within the area that had been cleared of snow by caribou or muskoxen. This method may underestimate the amount of lichens that was present in craters before they were grazed, because lichens in Cape Krusenstern did not often occur in thick mats, but were usually loosely interwoven with

moss and other vegetation and may have been completely removed by a grazing animal. In contrast, mosses and graminoids are not completely removed by grazing animals. Graminoids are typically bitten off a few cm above the ground. This leaves behind a base which covers approximately the same area as an ungrazed plant when viewed from above. Mosses have a solid base that is frozen or strongly attached to the ground, which stays behind after the top layer has been eaten. Percent cover of graminoids (Nellemann and Thomsen 1994) and lichens (Nellemann 1996) correlates closely with biomass and can be used as an indicator of availability. On the Seward Peninsula, craters that were grazed by reindeer and caribou or muskoxen did not differ in vegetation composition from random areas within feeding sites (Ihl and Klein 2001).

At the undisturbed edge of each crater, I measured snow depth with a metal ruler after clearing snow to the ground. I used a spring penetrometer (Skogland 1978) to measure vertical hardness at the least disturbed edge of each crater. At feeding sites with little or no snow, I examined the vegetation for signs of grazing such as cropped graminoids or moss. I then randomly selected 6 such grazed areas per feeding site, centered a 0.25m^2 frame over each area, and estimated vegetation cover within the frame. If no snow was present, I recorded snow depth and hardness as 0.

At each muskox or caribou feeding site, I collected a combined fecal sample of 6-10 pellets from 6 different pellet groups. At the Wildlife Habitat Management Laboratory, Washington State University, fecal samples were examined at 100 views per slide for the occurrence of major forage classes (Todd and Hansen 1973). I averaged

percent composition of moss in fecal samples from feeding sites within the same wintering area to represent forage selection at wintering areas.

A question central to this study is whether fecal collections reflect forage eaten in the same wintering area where they were collected. All six muskox groups in Cape Krusenstern remained within definable wintering areas, typically on hilltops and contiguous ridgelines, throughout the study period. One group left a wintering area near the coast in late March to join another group on a nearby hill, but I sampled feeding sites and collected fecal samples for both groups before they joined. I used established feeding sites, repeated observations of the location of each group, and the topographical features of each hill group to determine the wintering area used by each muskox group during the study period. I sampled 2-5 feeding sites on each wintering area and made observations of the location of muskox groups whenever I was able to visually locate a group while traveling during fieldwork. Observations of group locations ranged from 3 observations for the Tahinichok group to almost daily sightings of groups at Ingitkalik and Sealing Point, which were located closest to the field camp (Fig. 1).

I calculated muskox densities on wintering areas by dividing group size by the size of the wintering area used by each group. To estimate the size of wintering areas, I outlined the borders of each wintering area on a 1:63,360 scale topographical map. I then laid a grid divided into squares representing 0.01 km^2 over the outline and counted the number of km^2 enclosed by each wintering area.

I calculated terrain ruggedness on wintering areas using the terrain ruggedness index (TRI) devised by Nellemann and Thomsen (1994). I obtained this index by laying

a transect across a 1:63,360 scale topographical map with 15.2m (50ft) contour lines. The TRI incorporates elevation changes, which are expressed by counting the number of contour lines the transect crosses, as well as the total number of "ups and downs", or syn-and anticlinal changes along each transect. Because muskoxen foraged primarily near the tops of exposed ridges and hills, I laid each transect across the length-axis of ridges and allowed directional changes to follow ridgelines.

Because caribou groups were transient and much more mobile than muskox groups, I was unable to determine the total wintering area used by a given caribou group during the study period. Additionally, because I identified some feeding sites by following tracks rather than by sighting caribou, I could not determine exact group sizes to calculate caribou densities within wintering areas. Consequently, I calculated density and terrain ruggedness only for muskoxen.

I was unable to examine the complete extent of caribou movements, but on one occasion I observed a group of caribou on the same lower slope on three consecutive days, during which time the group established several feeding sites. Therefore caribou may remain in a wintering area long enough for defecations to reflect forage that had been eaten on feeding sites in the same wintering area. Consequently, I combined feeding sites that were established successively by the same caribou group into wintering areas. In this way, I re-grouped the 11 sampled caribou feeding sites into 7 caribou wintering areas.

2.43 Seward Peninsula

Sampling methods for snow conditions, vegetation cover, and fecal collections on muskox and reindeer or caribou feeding sites on the Seward Peninsula are described in Ihl and Klein (2001). For this study, I pooled fecal, vegetation, and snow data from Ihl and Klein (2001) according to individual muskoxen and *Rangifer* wintering areas. I combined *Rangifer* feeding sites into wintering areas and calculated size of muskox wintering areas, muskox density, and terrain ruggedness in a similar manner as described for Cape Krusenstern. In 1996 and 1997, I sampled vegetation cover, snow conditions, and fecal composition on 13 and 10 muskox feeding sites, respectively, which I combined into 5 and 6 muskox wintering areas, respectively. I obtained data on muskox density for 3 and 4 muskox wintering areas in 1996 and 1997, respectively, and terrain ruggedness for 4 and 5 muskox wintering areas in 1996 and 1997, respectively. I sampled 12 and 11 Rangifer feeding sites, respectively, in 1996 and 1997, and combined these into 6 *Rangifer* wintering areas for both 1996 and 1997 according to the criteria described above.

2.44 Data treatment and statistical analyses

I used 2-tailed t-tests with an assumption of unequal variances to test for regional differences in percent moss in muskox and caribou fecal samples from the Seward Peninsula and Cape Krusenstern. Within each region, I used single-factor ANOVAs to test for differences in fecal moss among winter areas. Because ANOVAs

cannot be run on single data points, I excluded those wintering areas for which I sampled only 1 feeding site.

I used linear regression analyses to test for relationships between fecal moss and wintering area conditions. For caribou, I regressed fecal moss against percent cover of lichen and moss and snow hardness and depth at feeding craters. For muskoxen, I ran regressions of fecal moss against graminoid and moss cover and snow hardness and depth at feeding craters, and terrain ruggedness and muskox density on wintering areas. Several muskox and caribou winter areas were represented by only 1 feeding site and therefore by only 1 fecal sample. However, because each fecal sample was itself a composite representing 6-10 individual defecations, I considered even a single fecal sample to be characteristic of feeding sites and included them in regression analyses. I conducted all analyses in Microsoft Office Excel 2003.

2.5 RESULTS

2.51 Local and regional differences in fecal moss

Fecal moss differed locally between individual muskox wintering areas in Cape Krusenstern ($F_{5,17} = 12.5$, $P < 0.0001$) but not on the Seward Peninsula ($F_{6,12} = 1.2$, $P = 0.4$). When I combined wintering areas for each region, there was no difference in percentage of fecal moss between the Seward Peninsula and Cape Krusenstern (Seward Peninsula: 34.3 ± 4.8%, Cape Krusenstern: 39.9 ± 9.7%, means±SE; $df = 7$, $t = -0.5$, $P = 0.6$).

In contrast, the percentage of fecal moss in caribou fecal samples did not differ locally among wintering areas on the Seward Peninsula ($F_{6,11} = 2.5$, $P = 0.09$) or in Cape Krusenstern ($F_{2,4} = 1.2$, $P = 0.4$), but there was a strong difference in the percentage of moss in caribou feces between the two regions (Seward Peninsula: 19.8 ± 2.0%, Cape Krusenstern: 57.0 ± 2.1%, mean±SE; $df = 15$, $t = 12.7$, $P < 0.0001$).

2.52 Forage availability

On muskox wintering areas, percentages of moss in feces related negatively to graminoid cover ($r^2 = 0.48$, $F_{1,15} = 13.8$, $P = 0.002$; Fig. 2.2a) and positively to moss cover ($r^2 = 0.63$, $F_{1,15} = 25.6$, $P = 0.0001$; Fig. 2.2b). On wintering areas of *Rangifer*, percentages of moss in feces did not relate to lichen cover ($r^2 = 0.16$, $F_{1,17} = 3.4$, $P = 0.08$; Fig. 2.2d), but related positively to moss cover ($r^2 = 0.33$, $F_{1,17} = 8.5$, $P = 0.01$; Fig. 2.2e).

2.53 Forage accessibility

On muskox wintering areas, percentages of moss in feces related positively to snow hardness ($r^2 = 0.75$, $F_{1,14} = 41.1$, $P < 0.0001$; Fig. 2.2c), but did not relate to snow depth ($r^2 = 0.0$, $F_{1,14} = 0.4$, $P = 0.56$). On *Rangifer* wintering areas, fecal moss percentages did not relate to either snow depth ($r^2 = 0.1$, $F_{1,17} = 1.0$, $P = 0.3$) or snow hardness ($r^2 = 0.0$, $F_{1,17} = 0.1$, $P = 0.8$; Fig. 2.2f).

2.54 Location

Percentages of moss in feces related to density of muskoxen on wintering areas ($r^2 = 0.45$, $F_{11,1} = 9.1$, $P = 0.01$). This relationship was driven by the six wintering areas in Cape Krusenstern, which all had densities > 2.3 muskoxen per km^2. When regressed separately, muskox densities on Cape Krusenstern wintering areas related strongly to fecal moss ($r^2 = 0.93$, $F_{1,4} = 54.0$, $P = 0.02$), while those on the Seward Peninsula did not relate to fecal moss ($r^2 = 0.2$, $F_{1,5} = 1.5$, $P = 0.3$) (Fig. 2.3a). Terrain ruggedness did not relate to fecal moss ($r^2 = 0.1$, $F_{1,13} = 1.5$, $P = 0.2$) (Fig. 2.3b). Hills used by muskoxen as wintering areas in Cape Krusenstern had steeper slopes and were generally higher in elevation than those on the Seward Peninsula (Fig. 2.4).

2.6 DISCUSSION

For muskoxen, my hypotheses that moss intake would be inversely correlated to graminoid availability and accessibility on wintering areas was supported. Similarly, the data support the hypothesis that moss use increases with muskox density on wintering areas, but I reject the hypothesis that terrain ruggedness of wintering areas correlates with a decrease of moss use in muskoxen. For caribou, however, I reject the hypotheses that moss use increases when lichens are less available or when snow depth and hardness increase.

2.61 Local and regional differences in fecal moss

During summer, muskox groups fuse and interact freely (Ihl and Barboza, in review), but during late winter, groups from the same population are isolated (Nellemann and Reynolds 1997, Ihl and Klein 2001), and each group may face very different foraging conditions. Consequently, fecal moss differed between individual muskox wintering areas. For caribou, such a fine-scale resolution may not be possible. Mean rumen retention times for winter diet in reindeer and caribou is approximately 23 hrs (White and Trudell 1980), and total retention times in the digestive tract for large ruminants are >70 hrs (Schaefer at al 1978). However, poorly digestible forages components such as moss may remain in the animal's digestive tract much longer (Staaland et al. 1988). It appears likely that ingested mosses do not leave the caribou's digestive tract until > 70 hours later, and caribou may have foraged on several wintering areas during that time. The association of caribou fecal samples with representative wintering areas must therefore be done at a larger, regional scale. Consequently, fecal moss in caribou differed between the two study regions, but not between individual wintering areas within each region.

2.62 Forage availability

Moss ingestion by Arctic ungulates is often considered to be an unavoidable cost when selecting preferred forages (Parker 1978, White 1983). Fruticose lichens frequently grow in association with moss, making it difficult for reindeer or caribou to select for lichens without ingesting moss. When preferred forages are low in abundance

or have been previously grazed, ungulates may ingest more moss in an attempt to obtain graminoid stem bases or finely dispersed lichens. Svalbard reindeer (*Rangifer tarandus platyrrhynchus*) ingest more moss on lichen-depleted ranges (Klein 1986, Staaland et al. 1993). Moss consumption at low forage abundance in Peary caribou (*Rangifer tarandus pearyi*) is correlated with decreasing fat reserves (Parker 1978, Thomas and Edmonds 1983). Although moss is a poorly digestible forage (Staaland et al 1988, Ihl and Barboza 2007), methodologies used so far to detect nutritional value of moss may have overlooked potential beneficial interactions that enhance digestibility of other forages (White 1983). Some mosses may also serve as a source of minerals (Staaland et al. 1988), while others may actually remove minerals from the animal (Ihl and Barboza 2007). It remains unclear, therefore, whether arctic ungulates ingest moss deliberately or merely tolerate moss ingestion as a cost of winter foraging. On many depleted wintering areas, moss may simply be the only forage available in large enough quantities to fill the rumen and alleviate hunger (Thomas et al. 1984). Consequently, moss use correlates with percent cover of moss in feeding craters in both species (Fig. 2.2b,e).

For caribou, there was a regional difference in moss use, with feces in Cape Krusenstern containing more moss than those on the Seward Peninsula. Although lichen cover did not significantly correlate with moss use on caribou wintering areas, lichen availability nevertheless appeared overall higher on the Seward Peninsula than in Cape Krusenstern: lichen in Cape Krusenstern did not tend to grow in thick, continuous beds as those on the Seward Peninsula, but rather tended to be more finely dispersed and

woven into the moss layer. This may have caused caribou to ingest more moss while foraging for lichens. In addition, because dispersed lichens scattered within the moss layer are visually conspicuous even in low amounts, I may have overestimated percent cover of lichens in feeding craters in Cape Krusenstern.

Caribou groups were smaller (10-30 animals) in Cape Krusenstern than those on the Seward Peninsula (up to several hundred animals). Cape Krusenstern lies along the migration route of the Western Arctic caribou herd and is not a traditional winter range (Dau 2005*b*), which may reflect the lower lichen availability and hence lower carrying capacity of wintering areas for caribou in Cape Krusenstern. A greater lichen biomass on wintering areas generally supports greater biomass and productivity of *Rangifer* (Kojola et al. 1995, Heggberger et al. 2002). Nevertheless, increasing numbers of caribou have wintered in Cape Krusenstern since the Western Arctic herd has grown to its peak size of 490,000 animals (Dau 2005*b*).

2.63 Forage accessibility

Because cratering through snow is energetically more costly than feeding on forage above the snow surface (Thing 1977), both muskoxen (Wilson 1992, Schaefer and Messier 1995*a*, Ihl and Klein 2001, Larter and Nagy 2001) and caribou or reindeer (Adamczewski et al. 1988, Collins and Smith 1991, Ihl and Klein 2001, Larter and Nagy 2001) seek areas of shallower and softer snow than surrounding areas to establish feeding sites. Snow hardness may be the most important criterion determining where arctic ungulates can feed in the winter (Ihl and Klein 2001). Grazing intensity within

feeding craters is generally light (Schaefer and Messier 1995*a*), but deep or hard snow may force ungulates to use established craters more intensely, which may deplete preferred forages and lead to an increased moss intake (Fig. 2.2c).

Caribou are more mobile, and their longer legs with shovel-shaped, hard hooves are better adapted to digging through snow than those of muskoxen (Klein 1992). Although caribou and reindeer, like muskoxen, seek out feeding areas with shallower and softer snow than random areas (Saperstein 1993, Larter and Nagy 2001), they are able to crater in deeper and harder snow than muskoxen (Biddlecomb 1991, Ihl and Klein 2001). Consequently, moss use by caribou may be driven to a higher degree by availability of forages and to a lesser degree by snow conditions than moss use by muskoxen. Consequently, percentages of fecal moss in caribou in Cape Krusenstern and on the Seward Peninsula did not correlate with snow hardness, and caribou in both regions cratered in greater range of snow hardnesses than muskoxen (Fig 2.2e,f). In Cape Krusenstern, caribou, unlike muskoxen, did not forage in areas where snow conditions were less severe, such as on hilltops, but established most feeding sites on lower slopes or in tussock tundra in the valleys, where lichen availability was higher. This resulted in a spatial separation of the two species. In contrast, on the Seward Peninsula, the generally lower and softer hilltops offered both a high lichen availability and shallower and softer snow than lower slopes and valley bottoms. Consequently both caribou and muskoxen were using hilltops on the Seward Peninsula, leading to spatial overlap (Ihl and Klein 2001).

2.64 Location

Fecal moss of muskox groups correlated with muskox density on wintering areas. The correlation was strongest on wintering areas that exceeded 2.3 muskoxen/km^2, most of which were located in Cape Krusenstern (Fig. 2.3a). Wintering areas in Cape Krusenstern were generally more spatially confined. The total area available to wintering muskox groups is in part determined by the topography of hill groups selected by muskoxen as wintering areas. In Cape Krusenstern, hill groups were generally abrupt, steep-sided, and taller than on the northern Seward Peninsula (Fig.2.4). Because slopes were steep, only the tops of hills and ridges and the uppermost part of slopes were used by muskoxen. The shallower slopes on the Seward Peninsula allowed muskoxen to use a greater altitudinal gradient and consequently a larger selection of vegetation types.

I observed no relationship between terrain ruggedness and moss use on muskox wintering areas; however, such a relationship may be sensitive to the spatial scale at which terrain ruggedness is measured. Nellemann (1996) reported a correlation between reindeer crater density and terrain ruggedness only at the smaller (10-20m contour lines on topographical maps) of two spatial scales measured. Although Nellemann and Reynolds (1997) were able to determine that muskox wintering areas are more rugged than surrounding terrain, a smaller spatial scale may be required to detect correlations between terrain ruggedness and forage selection between individual wintering areas. In Cape Krusenstern, flat, mesa-like hilltops with little terrain ruggedness like Ingitkalik (Fig. 2.4a) were typically almost completely blown free of snow, while the more rugged

profile of ridgetops such as Tahinichok (Fig. 2.4b) allowed snow to accumulate in small dips and on the leeside of bumps, creating a more varied snow profile. This may have prevented muskoxen from using some parts of the Tahinichok ridge, while the whole top of Ingitkalik was available for foraging. The vegetation type on both hills was partially vegetated *Dryas* heath with interspesed *Carex* spp. On a spatially confined wintering areas, an increase of terrain ruggedness therefore possibly decreases the available area for foraging.

2.65 Circumpolar comparison of moss use by caribou and muskoxen

Across the Arctic, moss use is generally highest in winter, when foraging opportunities are most restricted for both ungulate species (Fig. 2.5). Among muskoxen, low Arctic populations in Alaska exhibit higher fecal moss values than those from other Arctic regions (Fig. 2.5b). Because thick lichen beds typical of many lower Arctic wintering areas are absent in the High Arctic, it has been suggested that there may be a latitudinal increase in moss consumption by caribou (Klein 1986). Indeed, moss percentages in the rumen of Peary caribou (Parker 1978) and feces of Svalbard reindeer (Staaland et al. 1988, 1993) are among the highest for the species. Nevertheless, low arctic and sub arctic Alaskan caribou exhibit fecal moss concentrations that are similar to those of high arctic *Rangifer* (Fig. 2.5b).

Snow is likely to be more restrictive to both ungulates in the low Arctic than in the high Arctic (Klein 1992). High Arctic muskoxen are able to forage in low-lying sedge meadows throughout the winter (Klein and Bay 1990) and may be able to move

between habitats if forage becomes depleted. In contrast, muskox groups in northwestern Alaska are confined to their respective wintering areas as soon as snow accumulates (Klein et al. 1993, Ihl and Klein 2001).

I observed an example in Cape Krusenstern that may provide an insight as to the upper limit of tolerable moss intake for muskoxen. A group of 26 muskoxen fed at Sealing Point on the southwestern edge of Krusenstern Lagoon (Fig. 2.1) until late March 2001. Presumably, the group had entered the area in autumn, as is typical of groups in Cape Krusenstern (Ihl and Barboza, in review), to feed on strips of sedge meadows growing in shallow troughs between the beach ridges. By late March, the troughs had filled with snow and muskoxen cratered exclusively on the narrow ridges, which had low graminoid cover (8.4%). Their feces at this time contained 10.2 % graminoids and 76.0% moss. In late March, the entire group walked across frozen Krusenstern Lagoon and climbed Ingitkalik hill (Fig. 2.4a) from the northwest, a trek of ca. 12km. On Ingitkalik, they joined a group of 11 muskoxen whose feces at the time contained 59.2% graminoids and 17.6% moss and whose feeding craters contained 41.9% graminoid cover (Appendix 2.1, 2.2). However, such radical relocations by wintering muskox groups are untypical in northwest Alaska. When preferred forage becomes depleted and moss intake rises to intolerable levels, most muskox groups may not be able to afford the energetic cost of relocating if alternative wintering areas are too distant.

2.7 MANAGEMENT IMPLICATIONS

Managers can use fecal moss as an indicator of conditions at muskox wintering areas, such as graminoid availability and snow hardness. However, for caribou, inferences from fecal moss regarding wintering area quality are perhaps only relevant to larger spatial scales, such as in regional comparisons. An increase in moss in the winter feces of arctic ungulates may point to overgrazed ranges, severe snow conditions or crowded conditions on wintering areas. If snowfall increases in the future, a possible global warming scenario (Heggberger et al. 2002), Arctic ungulates may be further confined on wintering areas, which may lead to an increase in moss intake. Muskoxen may be forced onto windblown hilltops earlier in the winter, which will likely lead to greater forage depletion in late winter. Managers should be aware that muskoxen, unlike caribou, are spatially more restricted during late winter. Consequently, individual muskox groups may face very different foraging scenarios on their respective wintering areas. This may lead to heterogenous productivity within a muskox population if wintering areas are limiting. Such differences could be easily overlooked if muskoxen are surveyed only during summer months, after they have left wintering areas and groups have likely reorganized themselves. The topography and overall area of potential wintering areas should be considered when managing muskox populations that are expanding or shifting their ranges.

2.8 ACKNOWLEDGMENTS

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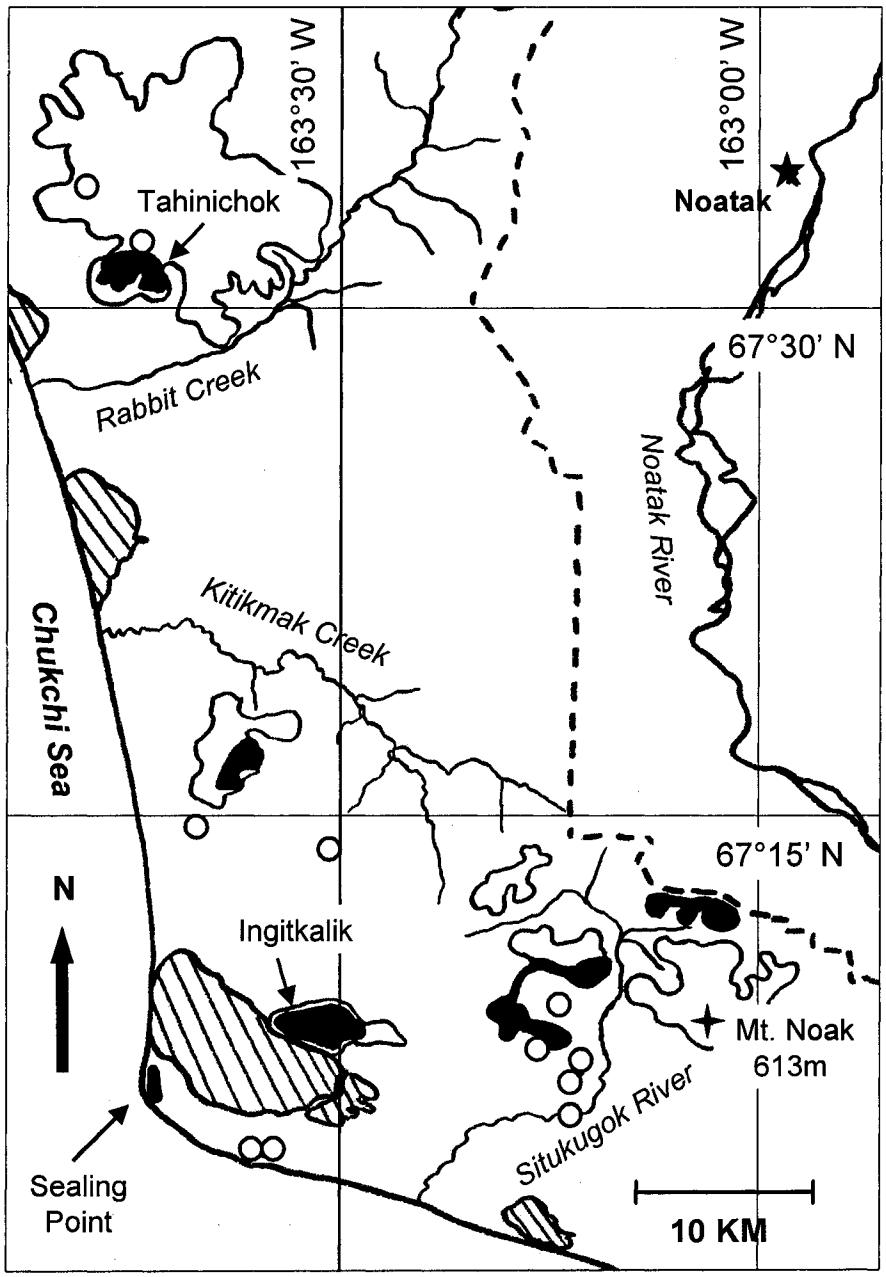

FIGURE 2.1: Study area in Cape Krusenstern National Monument, Alaska, USA. The dashed line shows the border of Cape Krusenstern National Monument. Hatched areas are coastal lagoons. Solid outlines are major hill groups. Solid black areas are muskox wintering areas and open circles are caribou feeding sites during March-May 2001.

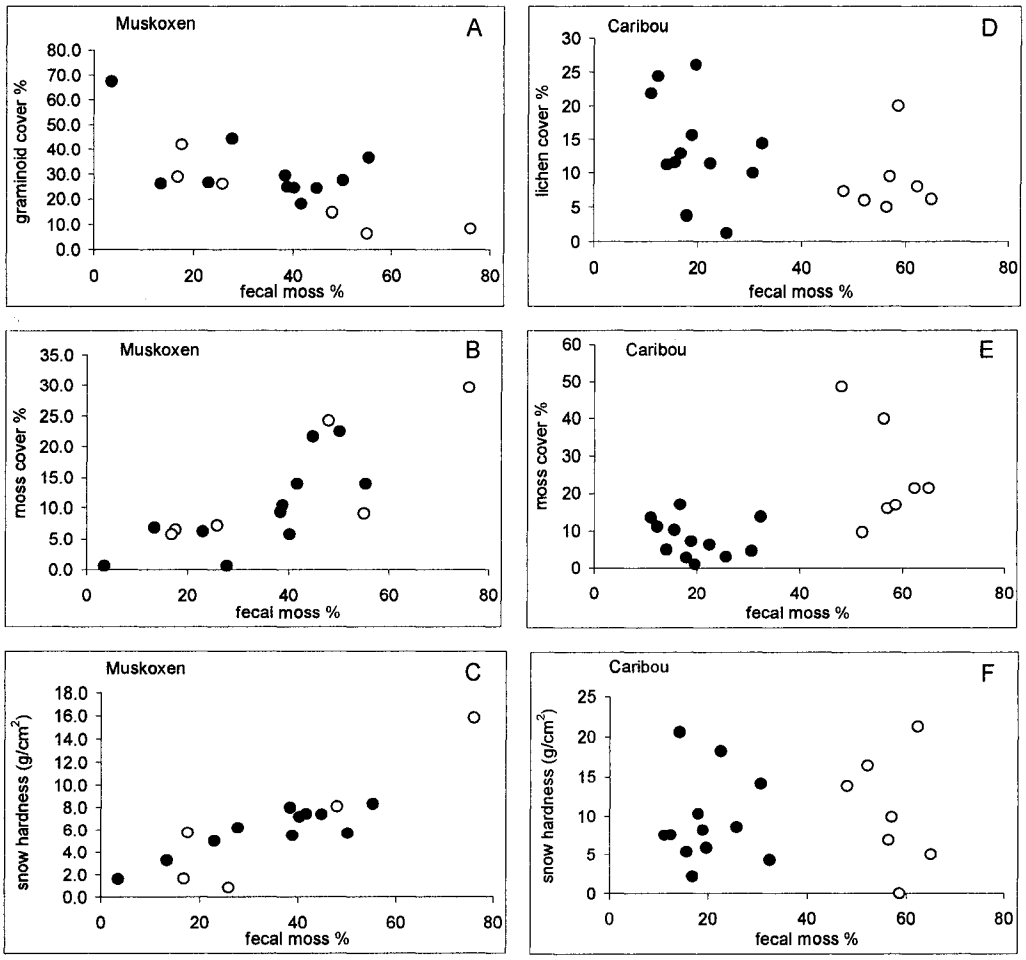

FIGURE 2.2: Relationship between fecal moss and percent cover of preferred forages (top row), percent cover of moss (middle row), and snow hardness (bottom row) at muskox and caribou wintering areas in northwestern Alaska, USA. Closed circles: northern Seward Peninsula (March and April 1996, 1997), open circles: Cape Krusenstern (March and April 2001).

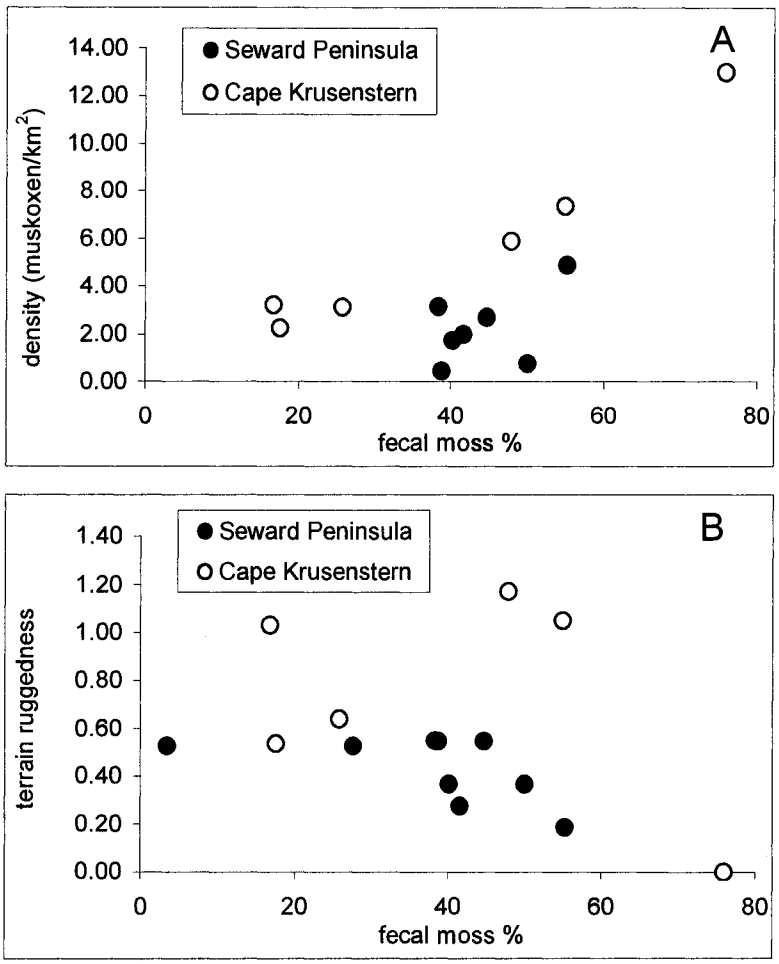

FIGURE 2.3: Relationships between fecal moss and muskox density (A) and terrain ruggedness (B) at muskox wintering areas in northwestern Alaska, USA. Closed circles: northern Seward Peninsula (March and April 1996, 1997), open circles: Cape Krusenstern (March and April 2001).

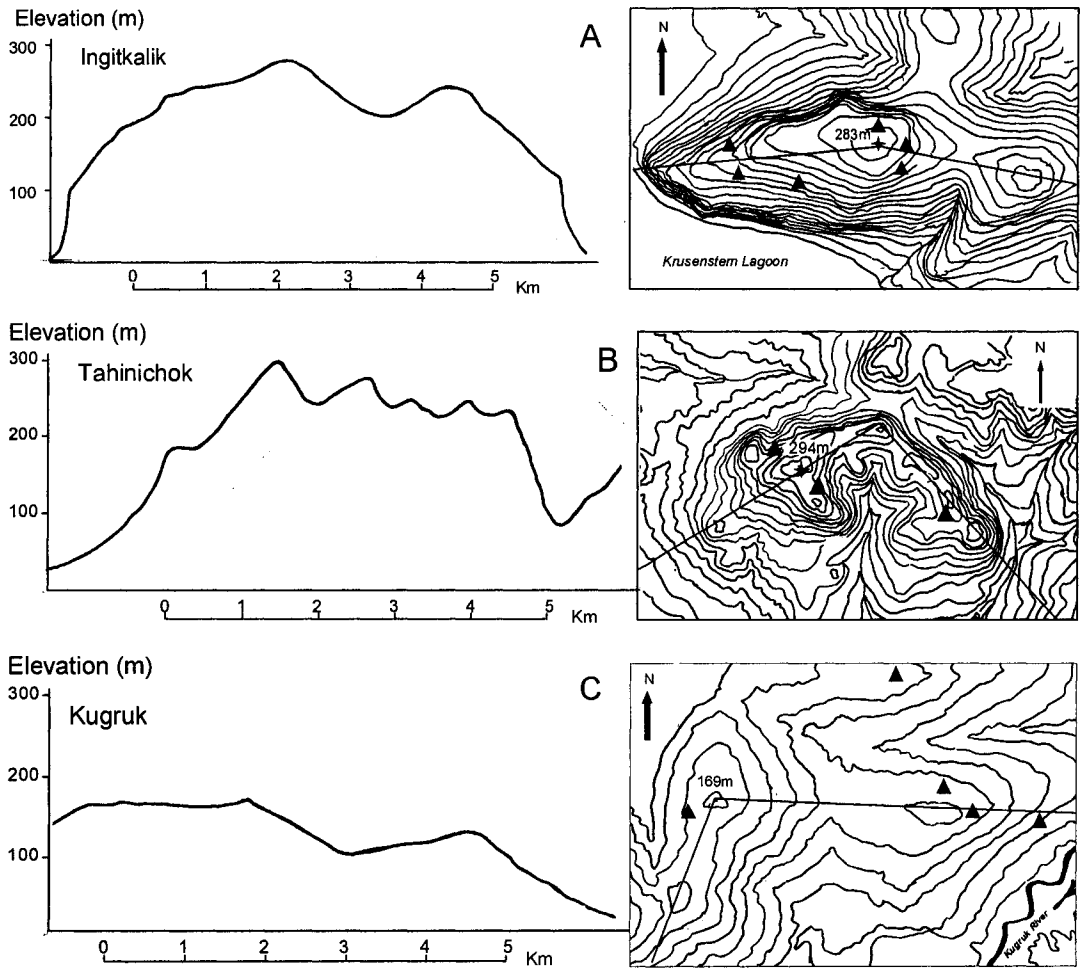

FIGURE 2.4: Profiles and topographic maps of 3 muskox wintering areas in northwestern Alaska, USA. Ingitkalik and Tahinichok are located in Cape Krusenstern National Monument and Kugruk is on the northern Seward Peninsula. Black triangles are muskox feeding sites sampled during March and April 2001 (Cape Krusenstern) and March and April 1997 (Seward Peninsula). Black lines trace the paths of wintering area profiles.

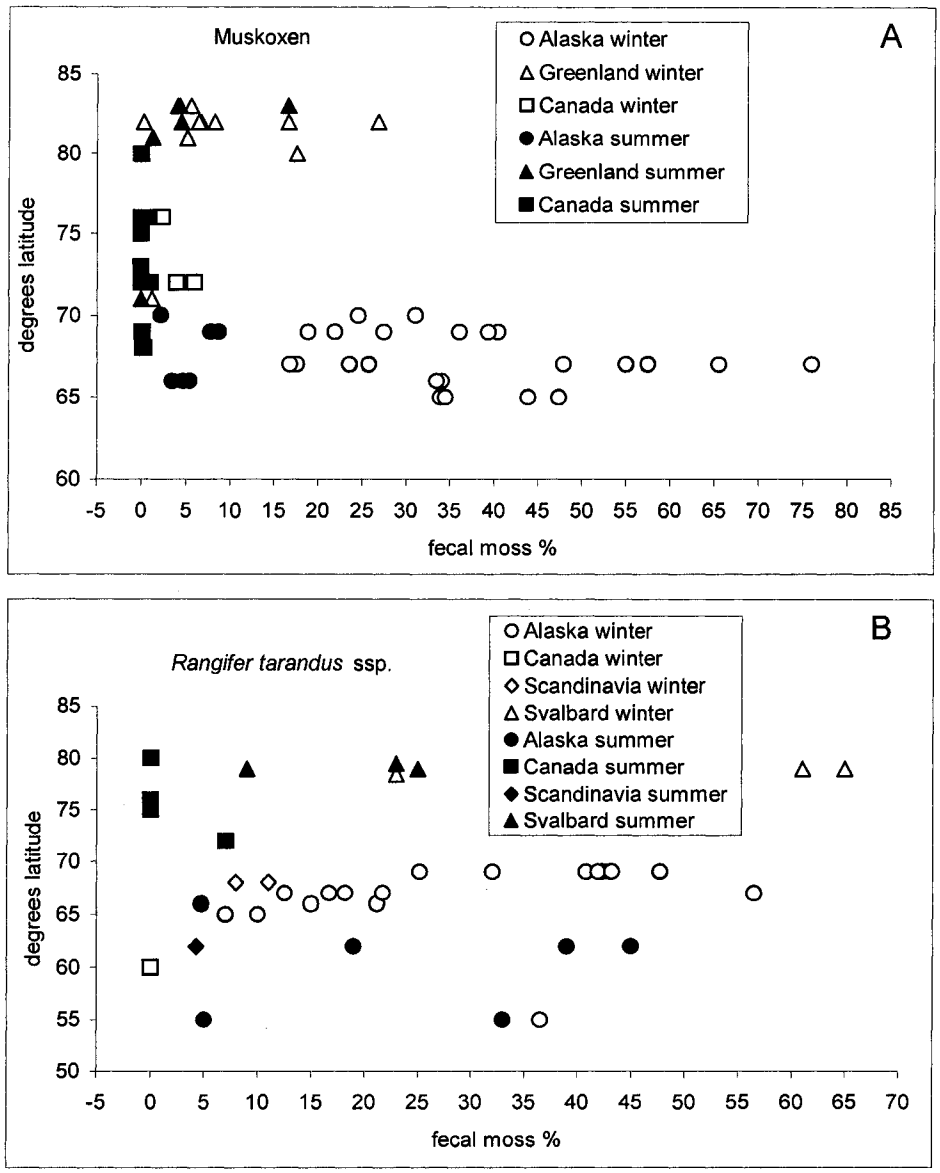

FIGURE 2.5: Percent moss in summer and winter feces of muskoxen (A) and *Rangifer tarandus* ssp (B) from various regions of the Arctic. Muskox data from: Biddlecomb 1991, Gunn and Sutherland 1997, Ihl and Klein 2001, Ihl unpublished data 1996, 1997, and 1999, Jandt 1992, Jingfors 1980, Klein and Bay 1990, Klein and Bay 1994, Larter and Nagy 1997, Oakes et al. 1992, Parker 1978, Robus 1981, Thing et al 1987, Wilson 1992, and this study. *Rangifer* data from: Barten et al. 2001, Biddlecomb 1991, Boertje 1981, Ihl and Klein 2001, Jandt 1992, Kojola et al. 1995, Larter and Nagy 1997, Parker 1978, Post and Klein 1999, Rominger and Oldemeyer 1990, Saperstein 1993, Skogland 1984, Staaland et al. 1993, and this study.

Appendix 2.1: Discernible plant fragments (100 views per slide) in muskox and caribou late winter fecal pellets in Cape Krusenstern National Monument during March and April 2001. Sample sizes are pooled fecal samples of 6-10 pellet groups. I collected one pooled sample per feeding site. For muskoxen, I pooled feeding sites located on the same wintering area. Means±(SE).

Location		N	Fecal composition					
Muskoxen			graminoids	moss	lichens	forbs	*Dryas* sp.	shrubs
	Akargichek	7	36.8 (6.1)	25.8 (6.1)	3.7 (1.0)	6.0 (1.1)	9.2 (2.0)	18.1 (2.1)
	Kakagrak	5	69.7 (5.7)	16.8 (3.9)	0.4 (0.2)	4.3 (1.2)	0 (0)	8.8 (1.7)
	Tahinichok	6	9.2 (1.3)	55.0 (2.6)	1.0 (0.5)	0.9 (0.7)	5.5 (1.6)	25.9 (2.2)
	Noak	5	29.0 (7.0)	47.9 (7.3)	1.3 (0.5)	3.2 (1.7)	1.7 (1.1)	16.8 (3.0)
	Sealing Point	7	10.2 (1.8)	76.0 (0.9)	7.8 (1.3)	1.7 (0.6)	0 (0)	4.1 (1.0)
	Ingitkalik	4	59.2 (2.5)	17.6 (2.7)	0.1 (0.1)	1.4 (0.4)	1.1 (1.1)	20.6 (3.6)
Caribou								
	Akargichek South	1	9.4	56.3	17.2	0	9.8	7.3
	Akargichek North	1	9.6	58.6	9.6	2.4	12	7.8
	Situkugok 1	1	7.2	52.8	25	1.6	3.3	10.1
	Situkugok 2	1	13.4	46.8	22.8	0.7	3.9	12.2
	Situkugok 3	1	7.3	71.3	9.6	0	0	11.8
	Lagoon 1	1	12.2	45.0	33.6	3.7	0	5.5
	Lagoon 2	1	5.8	51.1	29.6	1.7	11.2	0.6
	Tahinichok South	1	7.0	52.1	21.8	3.8	8.8	6.5
	Tahinichok North	1	3.1	65.0	12.7	0	8.6	10.6
	Eigaloruk 1	1	13.1	59.4	7.4	2.8	8.5	8.8
	Eigaloruk 2	1	6.5	65.2	19.5	0	0	8.8
Caribou total		11	8.6 (1.0)	56.7 (2.5)	19.0 (2.6)	1.5 (0.5)	6.0 (1.4)	8.2 (1.0)

Appendix 2.2: Parameters associated with muskox and caribou wintering areas in Cape Krusenstern National Monument during March and April 2001. Sample sizes are feeding sites. For muskoxen, I pooled feeding sites located on the same wintering area. Means±(SE).

Location	N	Animals		Vegetation cover			Snow conditions		Physical characetristics	
Muskoxen		Group size	Density (animals/area)	Graminoids	Moss	Lichen	Snow depth (cm)	Snow hardness (kg/cm^2)	Area (km^2)	TRI[a]
Akargichek	5	16	3.1	26.0	9.9	5.0	0.9	0.8	5.1	0.64
Sealing Point	4	26	13.0	8.4	33.8	2.7	8.3	15.9	2	0.00
Ingitkalik	3	11	2.3	41.9	11.9	7.6	4.9	5.8	4.8	0.54
Noak	3	33	5.9	14.7	35.3	8.1	2.3	8.1	5.6	1.17
Kakagrak	2	19	3.2	28.9	8.2	9.6	1.7	1.6	5.9	1.03
Tahinichok	6	42	7.4	6.3	9.1	8.1			5.7	1.05
Caribou										
Akargichek South	1	25		43.3	73.3	5.0	10.3	6.9		
Akargichek North	1	33		10.0	25.8	20.0	0.0	0.0		
Situkugok 1	1	unknown		22.5	46.7	11.7	7.5	8.3		
Situkugok 2	1	unknown		15.0	31.7	9.2	8.5	9.1		
Situkugok 3	1	unknown		25.8	32.5	7.7	7.3	12.4		
Lagoon 1	1	10		5.0	66.7	6.7	19.3	17.0		
Lagoon 2	1	unknown		5.0	62.0	8.0	15.5	10.8		
Tahinichok South	1	unknown		3.5	10.2	6.0	6.8	16.5		
Tahinichok North	1	12		15.0	63.3	6.2	4.7	5.1		
Eigaloruk 1	1	25		40.0	33.3	9.2	17.0	25.1		
Eigaloruk 2	1	unknown		27.5	46.7	6.8	11.5	17.5		
Caribou total				19.3	44.7	12.0	9.9	11.7		

[a] Terrain Ruggedness Index, after Nellemann and Thomsen (1994).

Appendix 2.3: Parameters associated with muskox wintering areas on the northern Seward Peninsula, Alaska, during March and April 1996 and 1997. Sample sizes are feeding sites. I collected one pooled fecal sample of 6-10 pellets per feeding site

and pooled feeding sites located on the same wintering area. Means±(SE). A summary of these data appears in Ihl and Klein (2001).

[a] Terrain Ruggedness Index, after Nellemann and Thomsen (1994).

Location	N	Year	Animals		Fecal moss (%)	Vegetation cover		Snow conditions		Physical characteristics	
			Group size	Density (muskoxen/ km^2)		Graminoids	Moss	Snow depth (cm)	Snow hardness (kg/cm^2)	Area (km^2)	TRI[a]
Cottonwood	2	1996	19		23.0	26.6	6.3	9.9	5.1		
Goldbug	1	1996	40		27.7	44.4	0.6	23.7	6.2		0.53
Kugruk	3	1996	5	0.45	38.8	24.8	10.4	13.2	5.5	11.1	0.55
Deering	3	1996	10	2.00	41.6	18.1	14.0	9.6	7.5	5	0.28
Burnt River	4	1996	20	1.74	40.2	24.5	5.8	10.2	7.2	11.5	0.37
Goldbug	1	1997	20		3.5	67.5	0.6	9.0	1.6		0.53
Kugruk	3	1997	30	2.70	44.8	24.4	21.7	7.0	7.4	11.1	0.55
Burnt River	1	1997	9	0.78	50.1	27.5	22.5	16.0	5.7	11.5	0.37
Cripple	2	1997	20	4.88	55.3	36.6	14.1	6.3	8.4	4.1	0.19
Arizona	2	1997	31	3.16	38.4	29.4	9.4	5.7	8.0	9.8	0.55
Lake Island	1	1997	19		13.4	26.3	6.9	1.4	3.3		

Appendix 2.4: Parameters associated with feeding sites of mixed groups of reindeer and caribou on the northern Seward Peninsula, Alaska, during March and April 1996 and 1997. Sample sizes are feeding sites. I collected one pooled fecal sample of 6-10 pellets per feeding site. Means±(SE). A summary of these data appears in Ihl and Klein (2001).

Appendix 2.4: Parameters associated with feeding sites of mixed groups of reindeer and caribou on the northern Seward Peninsula, Alaska, during March and April 1996 and 1997. Sample sizes are feeding sites. I collected one pooled fecal sample of 6-10 pellets per feeding site. Means±(SE). A summary of these data appears in Ihl and Klein (2001).

Location	N	Year			Vegetation cover		Snow conditions	
			Group size (estimate)	Fecal moss (%)	Lichen	Moss	Snow depth (cm)	Snow hardness (kg/cm^2)
Crossfox 1	1	1996	unknown	15.4	15.6	6.3	3.4	6.5
Old Glory	1	1996	3	14.1	11.3	5.0	7.5	20.6
Crossfox 2	1	1996	70	19.7	16.3	7.5	16.5	15.4
Crossfox 3	1	1996	unknown	21.4	15.0	8.1	3.8	2.9
Noyes Creek	1	1996	250	19.6	26.0	1.0	7.1	5.9
Fink Creek 1	1	1996	50	9.2	19.4	14.4	13.2	3.7
Fink Creek 2	1	1996	50	22	3.8	6.3	18.5	7.1
Burnt River	1	1996	unknown	12.3	24.4	11.3	8.5	7.6
Kugruk 1	1	1996	15	16.6	16.3	11.9	16	10.3
Kugruk 2	1	1996	250	10	36.9	16.3	16.6	9.4
Kugruk 3	1	1996	250	13.9	13.8	23.8	6.9	4
Kugruk 4	1	1996	30	3.7	20.6	2.5	8.3	6.6
Cripple 1	1	1997	400	26	13.1	8.1	8.5	12.9
Cripple 2	1	1997	400	35.3	6.9	1.3	22.3	15.4
Goldbug	1	1997	unknown	25.7	1.3	3.1	20.4	8.6
Pinnell 1	1	1997	50	22.2	3.8	3.1	13.6	7.6
Pinnell 2	1	1997	50	13.6	3.8	2.5	30.8	13
Kugruk 5	1	1997	30	18.5	8.8	6.3	15.4	30.8
Kugruk 6	1	1997	50	26.6	14.1	6.6	8.7	5.7
Fink Creek 3	1	1997	15	32.4	14.4	13.8	2.7	4.4
Deering 1	1	1997	400	10.8	10.0	34.4	0	0
Deering 2	1	1997	50	25.5	11.9	1.9	12.9	6.7
Deering 3	1	1997	50	14	16.9	15.0	0	0

CHAPTER 3

LEADERSHIP IN MIXED-SEX GROUPS OF MUSKOXEN DURING THE SNOW-FREE SEASON[3]

3.1 ABSTRACT

In social ungulates, particular individuals or cohorts, such as adult females, may lead or initiate foraging movements. We use muskoxen (*Ovibos moschatus*) as a model system to test hypotheses regarding the identity of leaders and the potential costs of leadership in three different behavioural contexts: activity initiation, foraging-bout movements, and spontaneous group movements. Adult females emerged as leaders in all three contexts, and other group members were more likely to follow adult females than adult males during initiations of activity. Males took a more active role during rut by provoking females to initiate group activity and by actively manipulating spontaneous movements led by females through herding and blocking activities. Leaders incurred no obvious costs in terms of lost foraging time. Costs and benefits of leadership may be subtle and difficult to measure in the field, and may include foraging and reproductive trade-offs as well as increased predation risk.

[3]Ihl, C., and R.T. Bowyer. 2007. Leadership in mixed-sex muskox groups during the snow-free season. Prepared for submission to Animal Behaviour.

3.2 INTRODUCTION

To maintain group cohesion, group-living animals in search of resources must reach a collective agreement on where to go. Such collective group decisions may be achieved in different ways. Couzin et al. (2005) modelled how movements of large groups are possible without direct leadership, as long as only a few "informed individuals" are present and all group members adhere to a few simple rules of movement. Such "leadership by numbers" (Couzin et al. 2005) may be the only group decision making process available to very large aggregations such as migrating wildebeest (*Connochaetes taurinus*) or fish shoals, where each group member can only communicate with its nearest neighbours. In small foraging groups of ungulates, however, where all members can communicate with each other, leadership and decision-making behaviours may be more complex and determined by social interactions (Conradt & Roper 2005). In smaller groups, individual animals (Dumont et al. 2005) or members of a particular sex-age group may serve as leaders of group movements (Reale & Festa-Bianchet 2003) or initiators of group activity (Leca et al. 2003). Prins (1996) observed what he termed "voting" among female African buffalo (*Syncerus caffer*) - animals standing up during resting bouts and positioning their bodies in a preferred direction of travel. Collective group decisions may not be equally advantageous for all group members because of differences in nutritional needs or reproductive status, and leaders themselves may pay a cost through lost foraging time or increased exposure to predators (Conradt & Roper 2003).

Studies of group leadership in social animals often are placed into three broad categories: theoretical models of potential mechanisms of group movements (Couzin et al. 2005, Ame et al. 2006) or costs and benefits to leaders and followers (Conradt & Roper 2003); experimental studies involving captive animals (Levin 1996, Lachlan et al. 1998, Reebs 2000); and, rarest of all, empirical data from free-ranging populations (Boinski 1993, Prins 1996, McComb et al. 2001), of which some are anecdotal observations (Miller et al. 1972).

A challenge to those studying group leadership is determining how leaders can be identified in the field. Leadership may depend on season or behavioural context. For example, in ungulates, leaders may emerge during spontaneous long-distance group movements but not during slow daily foraging movements (Dumont et al. 2005). A leader is traditionally considered to be the animal in the front of a group movement (Miller at al. 1972, Kiflawi & Mazeroll 2006). Although animals in the front position can direct group movements (Bumann & Krause 1993, Reebs 2000), positioning of leaders may be difficult to distinguish in slow foraging-bout movements (Dumont et al. 2005) and in small groups where all members can communicate with each other by visual, olfactory or auditory signals (Boinski 1993).

Muskoxen live in groups of typically 10-40 animals (Gray 1987, Heard 1992) in a variable environment that exhibits strong seasonality. Muskoxen groups tend to be non-migratory and inhabit the same area for many years (Gray 1987). In the Arctic, forage quality and quantity (Boertje 1981, Klein 1990, Klein & Bay 1990) and nutritional needs of animals (White 1983) undergo large seasonal changes, and animals can

enhance their fitness by making fine-scale decisions on where and when to feed (White 1983). Groups would benefit from the knowledge and memory of their most experienced individuals to maximize their seasonal foraging success. Knowledge of the identity of such group leaders and their role during group movements also is important for management of muskox populations, especially when setting hunting quotas on different sex-age classes. In mixed-sex foraging groups of ungulates, adult females may be the most likely leaders (Gray 1987, Prins 1996) because they are followed by their young (Rowell 1991) or because they have the greatest nutritional need (Barboza & Bowyer 2000, 2001) and are therefore motivated to lead foraging movements (White 1983).

Motivations for group movements can be nutritional, physiological, related to predation avoidance or sociality, or be motivated by a combination of those factors. Nevertheless, group movements by muskoxen differ in characteristics such as speed, distance covered, and activities of individuals during the movement. We identify leaders in groups of muskoxen in three different behavioural contexts: initiators of group activity after resting bouts (Boinski 1993, Leca et al. 2003), leaders (occupying the front position) of slow foraging-bout movements (Dumont et al. 2005), and leaders of apparently spontaneous group movements (Dumont et al. 2005). The latter are relatively fast movements and cover longer distances than those associated with foraging bouts. We test the hypothesis that leaders emerge during activity initiations and spontaneous group movements, but not during slow foraging-bout movements, when communication between group members may be more subtle. We further

hypothesize that females will be more likely to lead and are more likely to be followed than males, and that leaders incur a cost through reduced feeding time.

3.3 STUDY AREA

Cape Krusenstern National Monument is a 2670 km^2 area adjacent to the Chuckchi Sea coast in north-western Alaska (Ihl, in preparation) (Fig. 3.1). Vegetation throughout the monument is Arctic coastal tundra. Beach ridges and extensive lagoons characterize areas near the coast, and there are several groups of hills up to 613 m in elevation further inland, which are used as wintering areas by muskoxen. Hilltops are generally barren and windswept with *Dryas* heath and hummocky tundra dominating as contiguous bands along hill slopes. The groups of hills are separated by wide expanses of gently rolling tussock tundra. Winters are long and cold with frequent severe windstorms; summers are cool with most precipitation falling in August.

After extirpation from Alaska in the late 1800s (Lent 1999), muskoxen were re-established to northwestern Alaska in recent decades (Coady & Hinman 1984). In 1970 and 1977, 36 and 34 muskoxen, respectively, were released near Cape Thompson in northwestern Alaska. After growing slowly for the first two decades, the population began to increase steadily in the early 1990s (Dau 2005). The population subsequently stabilized at ca. 350-400 animals and spread south to occupy Cape Krusenstern National Monument.

3.4 METHODS

We followed free-ranging mixed-sex groups of muskoxen on foot during 5 June - 22 September, 2002. Data collection covered two seasons: spring-summer (11 June - 9 July, 2002) and rut (15 July - 22 September, 2002). Although mating generally does not commence until mid-August, we observed intense courtship and competitive behaviours by males as early as 15 July. After this date, we no longer observed more than one adult male per group. For this reason, we grouped data from the second one-half of July with the rutting period.

We defined a group as any number of animals who maintained coherence while moving and travelling together in the same direction. Repeated observations of the same animals were unavoidable because the study population numbered only about 160 animals. During summer and rut, muskox groups were transient and repeatedly broke apart and reformed into new groups. We considered any newly formed group a unique observation, even if it contained some of the same individuals as previously observed groups.

During summer, we collected data during two field trips: 11 June - 21 June and 5 July - 9 July. We sampled the rutting period in four field trips, 15 July - 23 July, 5 August – 13 August, 24 August – 3 September, and 16 September – 22 September. We initially located muskox groups from fixed-wing airplanes at the beginning of each sampling period. We then selected a location for our base camp and from there approached muskox herds on foot. We observed animals through a 20-60 x spotting scope and 8 x 40 binoculars from a distance of 100 to 1500 m. We considered groups

distinct as long as they were not interacting or travelling together. We observed each group as long as visibility, weather, daylight, and observer stamina allowed.

During June and July, observations included the diel cycle, but with most observations focused between 1000 hours and midnight. During all other times, we restricted observations to daylight hours only.

We determined age and sex of muskoxen on the basis of horn development, body size and coat length. We classified calves, yearlings, adult females ($\geq$ 2 years old), 2-year old males and adult males (Gray 1987). We placed 2-year old males in a separate category because while not reproductive, they remained within mixed-sex herds even during rut, indicating that their status in the group differed from that of non-reproductive adult males. We saw 2-year old females nurse young on several occasions and therefore grouped them with adult females.

Initiators of activity were animals that first rose, left the resting area of the group, and began a new activity after a resting bout. A successful initiation was one in which > 80% of herd members followed the initiator by also rising and joining in the activity. For each initiation, we recorded the time elapsed until 80% of the herd had followed the initiator. Leaders of foraging-bout movements were the animals occupying the front position when >80% of the herd was slowly moving in the same direction while foraging. Spontaneous group movements differed from foraging-bout movements in that animals were either running or walking the entire time that we made observations; these animals did not forage and typically travelled >100m in 1 minute. Leaders of spontaneous group movements were the animals initiating the movement and occupying

the front position. Spontaneous group movements were typically much faster and covered more distance than foraging-bout movements. For each spontaneous group movement, we recorded the destination of the group and the activity immediately following that movement.

We used group scans at 15-min. intervals (Altmann 1974) to describe behaviour of all group members. During scans we recorded the sex-age class of each individual and whether each animal was feeding, walking, standing, lying, or engaged in sexual or aggressive interactions (Gray 1987).

3.41 Data treatment and statistical analyses

Because our study population numbered only about 150 animals, and muskox groups were transient and repeatedly broke apart and reformed into new groups, repeated observations of the same animals were unavoidable. We saw recognizable individuals in as few as one and as many as five different groups. Because our sampling unit was the group, and the goal of our study was to characterize behaviour of individuals within a particular group context, no other sampling methodology was possible, especially in this remote arctic setting. We do not believe that repeated observations on the same animals in different groups markedly biased results.

We used the *G*-statistic (Sokal & Rohlf 1969) to test the observed distribution of leaders in all three contexts against a null model assuming equal distribution of leadership among all sex-age classes. Thus, the null model assumed that leadership by any sex-age class would not differ significantly from the proportion of that sex-age

class in the population. Similarly, in a small group with known individuals, we used the *G*-statistic to test whether leadership was equally distributed among individuals. We used a two-tailed t-test to compare lag times until the group followed male and female initiators of activity. We used the *G*-test with Yates correction to test for differential success between males and females when initiating activity bouts. We also used the *G*-test to examine potential costs of leadership by comparing active time spent feeding versus not feeding between leaders and non-leaders.

3.5 RESULTS

3.51 Population demographics and observational statistics

An aerial survey conducted in April 2002 counted 163 muskoxen living in Cape Krusenstern National Monument. (Western Arctic National Parklands, U.S. National Park Service, unpublished data). The study population contained 3% adult males, 56% adult females, 13% 2-year old males, and 29% yearlings and young during summer 2002, and 14% adult males, 40% adult females, 18% 2-year old males, and 28% yearlings and young during rut 2002.

During summer, we observed 24 mixed-sex groups during 13 continuous observation periods lasting from 15 to 525 minutes. During some periods, we could observe more than one group simultaneously. During the rutting period, we observed 14

mixed-sex groups during 21 continuous observation periods lasting from 75 to 660 hours.

We recorded 67 attempts to initiate group activity after resting bouts by group leaders. Of these, 54 ($N = 23$, spring-summer and 31, rut) were successful. We observed 124 foraging-bout movements by muskoxen, during which >80% of the group travelled in the same direction. Foraging-bout movements comprised 29% ($N = 73$, spring-summer and 51, rut) of group scans taken during activity bouts. We observed 45 spontaneous group movements ($N = 25$, spring-summer and 20, rut).

3.52 Initiators of group activity

Adult female muskoxen were initiators of group activity (Fig. 3.2, top row) both in spring-summer ($G_3 = 22.6$, $P < 0.001$) and rut ($G_3 = 21.9$, $P < 0.001$). During rut, however, adult males also initiated more activity bouts than expected (Fig. 3.2, top row).

Females were more likely to be followed by group members than males ($G_1 = 3.95$, $P < 0.05$; Table 3.1). Nonetheless, successful initiations by males or females did not differ in the amount of time it took for > 50% of the group to follow (two-tailed *t*-test, $t_{11} = -0.79$, $P = 0.45$; Table 3.1). Although females always initiated activity bouts by beginning to forage, 40% of male initiations involved aggressive or sexual behaviour towards other group members (Table 3.1).

3.53 Leaders of foraging-bout movements

Leadership of foraging-bout movements differed from a random pattern in spring-summer (G-test: $G_3 = 39.3, p < 0.0001$) and rut (G-test: $G_3 = 35.5, p < 0.0001$). During spring-summer, adult females led 81% of observed foraging-bout movements, and observed leadership by females >30% higher than expected values ($N = 59$ vs 36). During the rut, adult males leading foraging-bout movements exceeded expected values by >50% ($N = 18$ vs 8), whereas adult females led more movements overall, but numbers were not greater than expected ($N = 27$ vs 24) (Fig. 3.2, middle row).

3.54 Leaders of spontaneous group movements

Adult females dominated as leaders of spontaneous group movements (Fig. 3.2, bottom row) in both spring-summer (G-test: $G_3 = 25.6, P < 0.0001$) and rut (G-test: $G_3 = 18.6, P < 0.0001$). Only one spontaneous group movement in spring-summer and two during rut were led by males (Fig. 3.2, bottom row).

During spring-summer, 36% of spontaneous group movements led to a new feeding area, 16% led to an area where the group rested, 24% resulted in the joining of another group, and 24% were unsuccessful in that <80% of the group followed, thereby resulting in a split of the group (Table 3.2). During rut, 50% of spontaneous movements were blocked or interrupted by the dominant male in the group (Table 3.2, Fig. 8), and only 30%, 10%, and 10% led to feeding and resting areas or the splitting of the group, respectively (Table 3.2).

3.55 Leadership by individuals

In a small group with 7 known individuals (1 adult male, 3 adult females, 1 2-yr old female, 2 young) that we observed during rut, leadership among all adult members did not differ from a random pattern during 13 activity initiations (G-test: $G_4 = 0.48$, $p = 0.98$) and 12 spontaneous group movements (G-test: $G_4 = 3.94$, $p = 0.41$) (Fig. 3.3). Nonetheless, during 23 foraging-bout movements (G-test: $G_4 = 16.49$, $p = 0.002$), the dominant male led more often than expected from a random pattern (Fig. 3.3).

3.56 Cost of leadership

Initiators of group activity and leaders of foraging-bout movements of either sex did not spend less time feeding than non-leaders of the same sex (Fig. 3.4). This outcome indicates that leaders did not pay a significant cost in terms of lost feeding time after initiating activity bouts (females: G-test: $G_1 = 0.58$, $p = 0.45$; males: G-test: $G_1 = 2.13$, $p = 0.14$) or while leading foraging-bout movements (females: G-test: $G_1 = 0.88$, $p = 0.35$; males: G-test: $G_1 = 0.1.10$, $p = 0.29$). Nevertheless, for males that initiated activity, the difference in time spent feeding versus non-leaders (29% versus 56% of total active time) approached significance.

3.6 DISCUSSION

Our data indicate that in muskoxen, group decision making is not a random process but that adult females lead more often (Fig. 3.2) than other sex-and-age classes, an observation that has been observed in taxa as diverse as fish (Kiflawi & Mazeroll,

2006), other ungulates (Prins 1996, Dumont et al. 2005), and primates (Boinski 1993, Leca et al. 2003). Leadership differed from random patterns in all three behavioural contexts we studied. This outcome supports our hypotheses that leadership would emerge during activity initiation and spontaneous group movements, but is in contrast to our hypothesis that the lead position during foraging bout movements would be occupied randomly (Fig. 3.2). The prominence of females as group leaders was most pronounced during spontaneous group movements (Fig. 3.2). These movements, more so than foraging-bout movements or activity initiation, had the potential to change the situation of the whole group, because they either led to new feeding areas, resting areas, or resulted in the fission or fusion of muskox groups (Table 3.1). Females thus carry much of the responsibility in determining where the group feeds, rests, and whether it will join another group. Female African buffalo also dominanted group movements by "voting" for their preferred direction during resting bouts. We did not quantify muskox positioning during resting bouts to determine whether muskoxen also "vote".

Although limited, data on the role of individuals in leadership indicated that the leadership role is not dominated by one individual, but tends to be shared by all adult females in the group during activity initiation and spontaneous group movements. An exception is the dominant muskox male, which during rut led 52% of all foraging movements (Fig. 3.3). In contrast, Dumont et al. (2005) observed the same individual in a group of 15 domestic heifers lead 48% of spontaneous group movements, but reported no such leadership during foraging-bout movements. Rowell (1991) observed that flocks of domestic sheep were led by the oldest ewe in 82% of observations.

Leadership patterns in muskoxen undergo seasonal changes. During rut, adult males took a more active role in all three movement types we studied. Rutting males initiated changes in group activity 43% of the time by provoking females to commence courtship or to chase females or other males (Table 3.2). Males were particularly active in interrupting attempts at spontaneous group movements initiated by females during rut. Males took advantage of topographic features such as coast lines, willow (*Salix* spp.) thickets, or rock outcroppings when attempting to block and manipulate female movements (Fig. 3.5), and typically continued that harassment until females abandoned their attempt to move in their initial direction. During foraging movements following such repeated interruptions, females often followed the male, presumably because any other movement attempt would be aggressively opposed by the male (Table 3.2, Fig. 8). In areas of high muskox densities, male-to-male competition for females might also lead to fission of groups during rut (Gunn 1992).

Theoretical models of group leadership (Conradt & Roper 2003; Conradt & Roper 2005, Couzin et al. 2005, Ame et al. 2006) rely on estimating the potential costs and benefits to leaders and followers. Conradt & Roper (2003, 2005) hypothesized that leaders should be the individuals with the highest consensus costs, for which following would be more costly than leading, while followers should be those group members for which following was less costly than either leading or making solitary movements. Nevertheless, we detected no significant difference in time spent feeding among leaders versus non-leaders of either sex in muskox groups (Fig. 3.4). Perhaps leadership costs are subtle and have to be measured at a much finer scale of foraging or in a different

currency, such as predation risk (Bumann et al. 1997). Wolves are most successful in hunting muskoxen if they succeed in enticing the group to give up their defensive formation and run, in which case the animals in the rear may be the most vulnerable (Mech 1988, 2007). Estimation of the costs of leadership is difficult to quantify among free-ranging animals in the field, and resolution of this question may be better addressed by an experimental approach with captive animals and using settings in which predation risk can be simulated.

A remaining question in studies of group leadership is how the transfer of information from leaders to followers occurs: how do group members determine which individuals to follow (Reebs 2000, Conradt & Roper 2005)? In some animal societies, leaders use specialized signals to relate information, such as the location of food sources to group members (von Frisch, 1967). Nonetheless leadership is possible without a transfer of information to followers (Couzin et al. 2005). Except for conflicts in leadership when leaders vocalize (see below), female leadership in muskoxen appears to be mostly passive because females do not apparently transfer information or otherwise entice other group members to follow; certainly they used no specialized behaviours for this purpose. Adult females may simply move first because they are the most experienced and therefore most confident group members or have the greatest physiological drive to forage. The costs of following should be lowest among members of the same sex-age group because they share similar nutritional needs and foraging strategies (Barboza & Bowyer 2000, 2001). Therefore, females should follow other females, resulting in synchrony of movement in muskox groups, which are typically

dominated by adult females. In such an instance, cost differences between leaders and followers may be very small. Such strong cohesion among female group members may be further enhanced in social ungulates with prolonged mother-daughter associations, where small groups may consist of female kin and older females which have automatic followers in their daughters (Green at al. 1989, Rowell 1991, McComb et al. 2001). Female young may thus learn from their mothers how to be future leaders (Klein 1999). This female-young association may explain why groups followed female initiators of group activity more often than male initiators (Table 3.1).

In contrast to females, males lead by actively manipulating the movements of other group members during rut. The main motivation of males during rut is not foraging, but to keep oestrous females under their direct control and prevent access of competing males to females (Gray 1987). A possible cost of increasing social interactions with females and other males is a loss of feeding time. Male activity initiators spent 26% less of their active time feeding compared to male non-leaders, a difference which approached statistical significance ($p = 0.14$). The presence of adult males in muskox groups during spring-summer was lower than during rut, and males had almost no role in group leadership during that time (Fig. 3.2). Because of their larger body size, adult male ungulates have different nutritional needs than females (Barboza & Bowyer 2000, 2001) and are less vulnerable to predation as long as they remain within groups. Outside of rut, it may be less costly for males to move alone or in small bachelor groups than to follow groups of females. Adult males that stay with

female groups outside rut typically exhibit less synchrony with the group than females (Cote et al. 1997).

Occasionally, leadership conflicts occurred when two females moved in different directions, each followed by a portion of the group, or when one female moved away, but only a part of the group followed her while the rest remained stationary. During such events, the leading female(s) frequently vocalized and occasionally ran back-and-forth several times in an apparent attempt to entice more group members to follow. At no time, however, did we observe females blocking or manipulating the movements of the group in the way bulls did during rut. Typically, such leadership conflicts resulted in the fission of the group (Table 3.2).

We conclude that females predominated as leaders of group movements and determined which feeding and resting areas groups use. Female leadership also influenced group sizes because in some instances it resulted in the fission or fusion of groups. Males, however, interfered with female leadership by actively blocking or manipulating group movements during the rut. Leadership costs are likely subtle and may vary depending on the nutritional, physiological and hormonal status of individuals. Costs may have to be measured in a different currency than time spent feeding.

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TABLE 3.1: Sexual differences between successful and unsuccessful initiations of group activity by male and female muskoxen, time until group follows initiators, and behaviour of activity initiators in mixed-sex muskox groups. Cape Krusenstern National Monument, Alaska, USA, June-September, 2002

	Activity initiators			
	Females		Males	
	N	%	N	%
Activity initiations[1]				
Successful[2]	46	86.8	8	57.1
Unsuccessful	7	13.2	6	42.9
Behaviour of leaders during activity initiation				
Foraging	53	100	8	57.1
Aggression towards males	0	0	1	7.1
Aggression towards females	0	0	5	35.7
	min (X ± SE)		min (X ± SE)	
Lag time until group follows	16.6 ± 2.0		20.1 ± 4.0	

[1] Differs between males and females ($G = 3.95$, $p < 0.05$, 1 df)
[2] We defined an activity initiation as successful if ≥ 80% of the group followed the initiator

TABLE 3.2: Outcome of spontaneous group movements by mixed-sex muskox groups, Cape Krusenstern National Monument, Alaska, USA, June-September, 2002.

destination/outcome of spontaneous group movement	Season			
	Spring/summer		Rut	
	N	%	N	%
move to new feeding area	9	36	6	30
move to resting area	4	16	2	10
group joins another group	6	24	0	0
group splits	6	24	2	10
movement interrupted by adult male	0	0	10	50

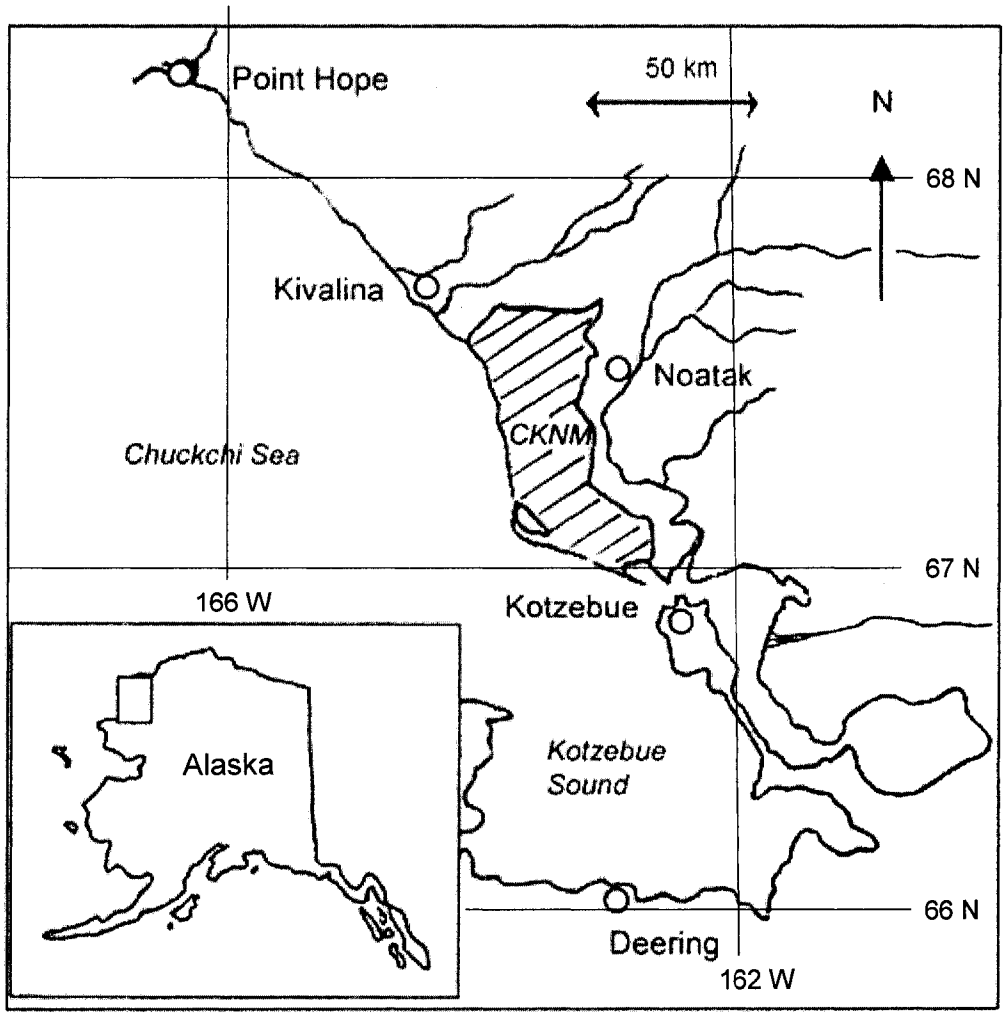

FIGURE 3.1: Location of Cape Krusenstern National Monument (CKNM) in north-western Alaska.

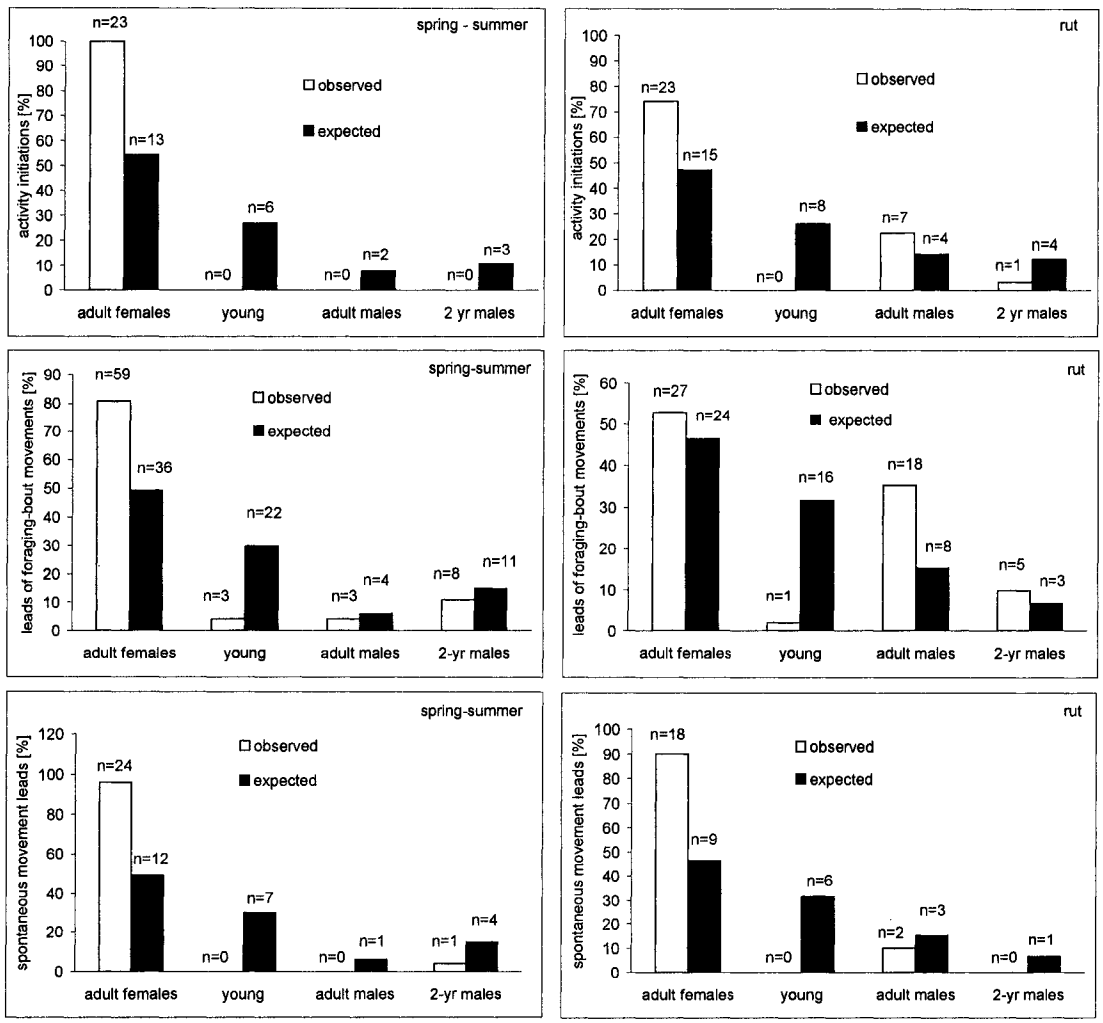

FIGURE 3.2: Group leadership in muskoxen in three behavioural contexts. Top row: activity initiations; middle Row: foraging-bout movements; bottom row: spontaneous group movements. Cape Krusenstern National Monument, Alaska, USA, June-September, 2002.

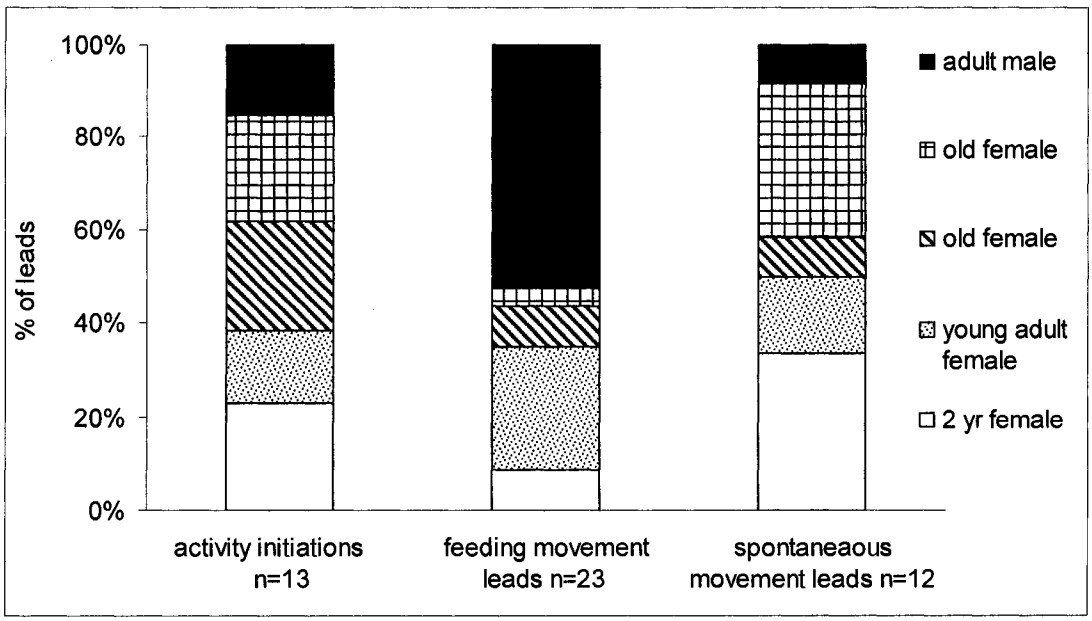

FIGURE 3.3: Distribution of leadership during activity initiations, foraging-bout movements, and spontaneous group movements among the five adult members of a free-ranging muskox group during the rut. Cape Krusenstern National Monument, Alaska, USA, June-September, 2002.

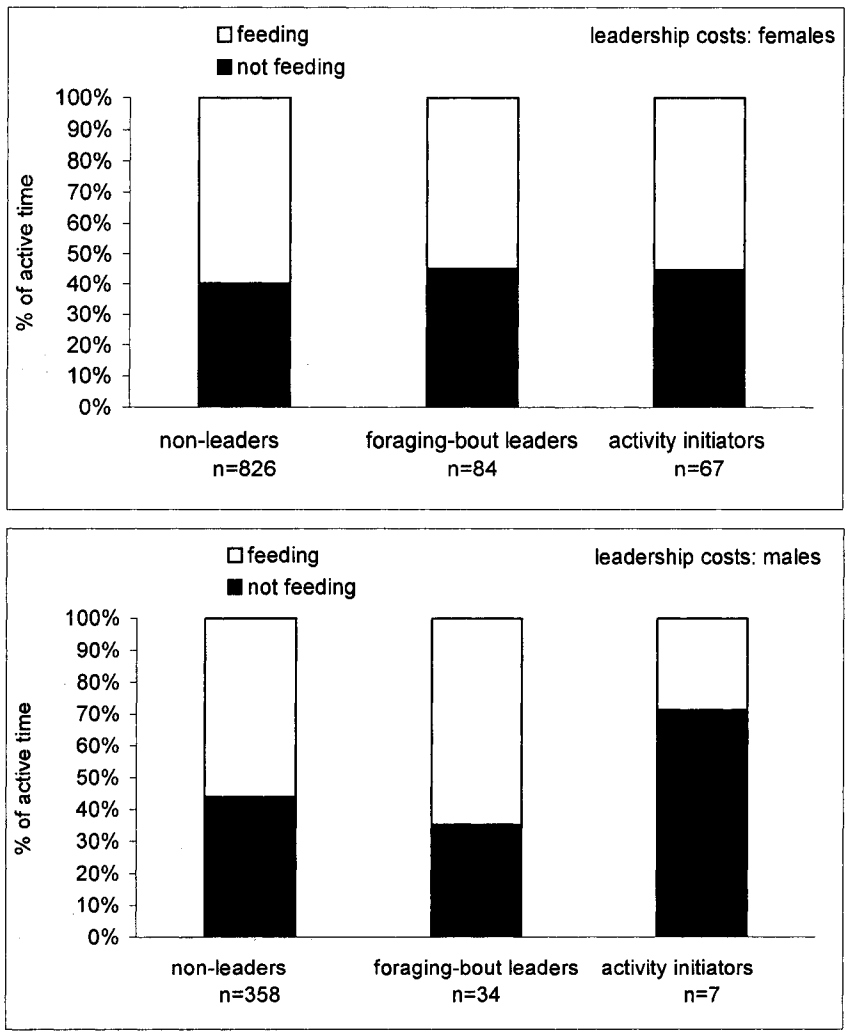

FIGURE 3.4: Active time spent feeding by non-leaders and leaders of activity initiations and foraging-bout movements in muskoxen. Cape Krusenstern National Monument, Alaska, USA, June-September, 2002.

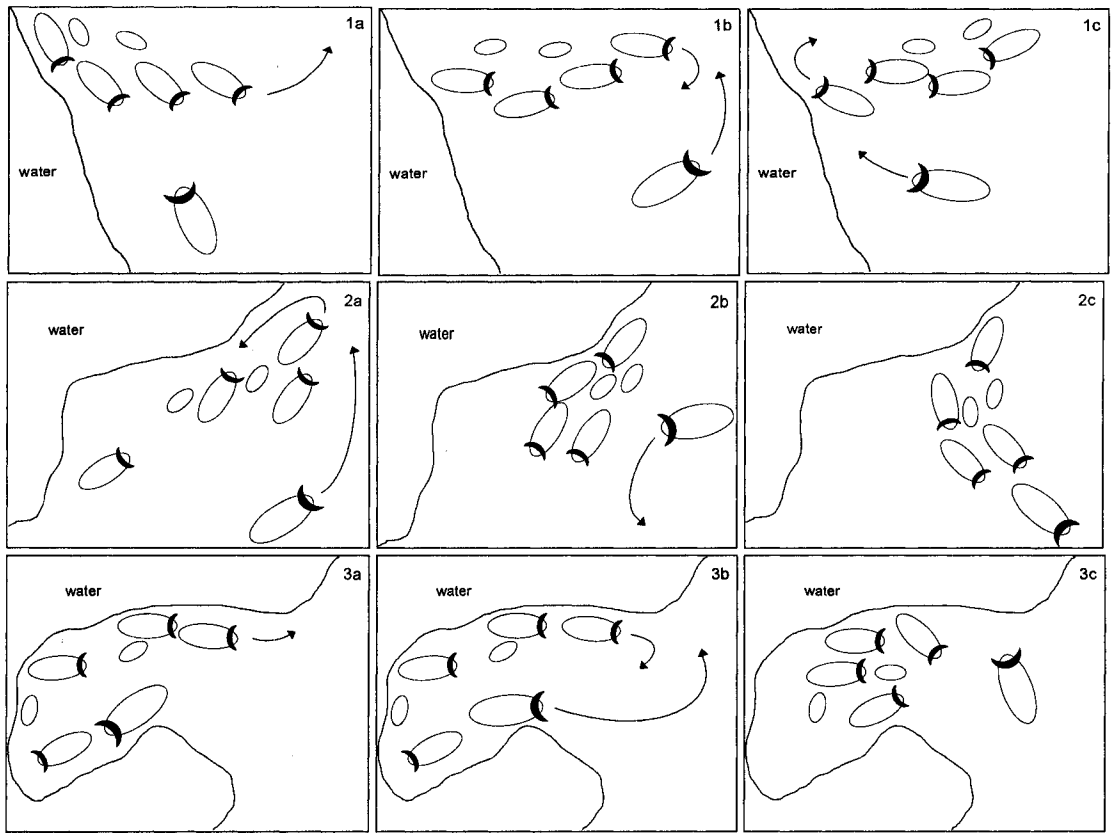

FIGURE 3.5: Three examples how a herd bull manipulated movements of females in a breeding harem of muskoxen in Cape Krusenstern National Monument, Aug 25-Sept 1, 2002.

1. Top row: a) females and calves move inland from the beach while bull is lying down. b) Bull rises and runs to cut off females. c) females turn around and bull cuts them off again at the beach. Females then abort movement attempt.

2. Middle row: a) females travel along the beach. Bull overtakes lead female and cuts them off. Females turn around. This is repeated four times. b) Females abort movement attempt and stand together while bull guards them. c) Females follow as bull leads a foraging movement inland.

3. Bottom row: a) The group forages on grasses on a sand spit. Females move up the beach while bull forages. b) Bull swings around and runs to cut off path of lead female. Lead female turns back into sand spit. c) Bull lies down at entrance of sand spit, preventing females from leaving.

CHAPTER 4

FISSION AND FUSION IN MUSKOX GROUPS[4]

4.1 ABSTRACT

We investigated group formation and group sizes in a free-ranging muskox (*Ovibos moschatus*) population in northwest Alaska, USA, between June and September, 2002. Seasonal habitat use by muskoxen shifted from dryas (*Dryas* spp.) and hummock slopes in early summer towards strips of sedge meadow during rut. *Dryas*, hummock and tussock habitats were spatially unbounded because they ran continuously over many km^2, while sedge meadows and willow thickets were spatially bounded to narrow strips in drainages and along beaches. Muskox groups decreased in size from winter to summer to rut. Muskoxen foraging efficiency (percent of active animals feeding) decreased with group size in spatially unbounded habitats, but not in spatially bounded habitats. Adult males contributed least to group cohesion. Group sizes were unrelated to percentage of males in the group during summer, but the presence of adult males may contribute to group fission during rut. We present a conceptual model in which we discuss how habitat, foraging, social behavior, and predation contribute to the fission and fusion of muskox groups.

[4]Ihl, C. , and P.S. Barboza. 2007. Fission and fusion in muskox groups. Prepared for submission to Canadian Journal of Zoology.

4.2 INTRODUCTION

Seasonal changes in group size have been observed in many species and are considered to be a response to changes in predation pressures (Hamilton 1971, Rubenstein 1978, Heard 1992), the availability and distribution of forage (Jarman 1974), social factors such as mating systems (Gunn 1992) or sex and age structure (Alexander 1974), animal density (Raman 1997), or a combination of factors. Group formation is consequently subject to opposing selective pressures that require compromise, such as benefits derived from decreased predation risk and costs incurred through competition for forage (Molvar and Bowyer 1994) or increased parasite transfer (Whiteman and Parker 2004).

Many animals live in open fission-fusion societies in which groups readily join and split up. These include primates (Henzi et al. 1997), cetaceans (Chilvers and Corkeron 2002), ungulates (Raman 1997, Cross et al. 2005, Foccardi and Pecchioli 2005) and birds (Keys and Dugatkin 1990). Groups remain stable only as long as group members synchronize their movement; factors leading to asynchronous behavior among group members result in the splitting of groups (Conradt and Roper 2000). Because group sizes of many ungulates change seasonally (Reynolds 1993, Raman 1997, Bowyer et al. 2001), selection pressures influencing group fission and fusion likely also differ across seasons.

Herbivores on Arctic ranges face extreme seasonal changes in forage availability and quality (Boertje 1981, White 1983, Klein 1990) and predation pressure (Heard 1992). Arctic ungulates must adapt their patterns of group formation to these changes to

meet individual physiological needs, which depend upon season, age, sex and reproductive state.

Muskoxen are a suitable subject for the study of intrinsic and extrinsic factors controlling group formation. These large herbivores live in variable environments that are highly seasonal (Klein and Bay 1990, Klein 1992), generally exist at low densities (Klein 1992), have an open fission-fusion society with variable group sizes (Tener 1965, Reynolds 1993, Gray 1987), and depend on group defense against predators (Gray 1987), which requires groups to maintain a high degree of cohesion.

We studied a population of muskoxen at Cape Krusenstern National Monument in northwest Alaska, USA. In this area, *Dryas* heath and hummocks typically form broad (> 1km) bands around hill slopes with tussocks filling valleys between hill groups. We therefore defined these habitats as "unbounded", because they ran continuously over many km^2 of slopes and around hills (Ihl, in preparation).
In contrast, willow and sedge meadows occurred in spatially confined patches usually no more than 100m wide in small drainages or along narrow strips of beach near the coast. Consequently, we defined willow and sedge habitats as "bounded". Bounded habitats are, however, rich in forage biomass because they are either composed of large woody plants (willow) or contain a high percentage of relatively productive graminoids (sedge). In contrast, lower biomass is spread over a larger area in unbounded habitats, particularly in dryas habitats, which are only partially vegetated. Due to the spatial extent of these habitats, grazing intensity is, on average, relatively low, resulting in an

unbounded forage supply, albeit at a relatively low biomass per m^2 compared with more productive habitats.

Arctic ungulates follow a phenology gradient throughout the growing season to maximize energy and protein intake (White 1983). Therefore, habitat use can be expected to change seasonally. We predict that group sizes of muskoxen adjust to reflect seasonal habitat use. When feeding in unbounded habitats with evenly distributed forage, muskox groups should be larger than when feeding in spatially bounded habitats (Gunn 1992, Klein and Bay 1990, 1994).

In many group-living ungulates, foraging efficiency is positively correlated with group size (Berger 1978, Raman 1997, Bowyer et al. 2001, Bowyer and Kie 2004), because individuals often spend less time in surveillance for predators in larger groups (Childress and Lung 2003). We predict that group foraging efficiency in muskoxen will increase with group size in spatially unbounded habitats but decrease with group size in bounded habitats.

Muskoxen differ from many other ungulates in that some adult males remain with female/young groups outside of the rut (Gray 1987). Cote et al. (1997) reported that in muskox groups, adult males exhibited less synchrony of activity than other sex-age classes. During rut, herd bulls guard harems of females and attempt to isolate them from other bulls (Ihl and Bowyer, in preparation, Smith 1976, Gray 1987). Consequently, the presence of adult bulls in groups, or a high density of bulls in the population (Gunn 1992), can be expected to reduce group cohesion and promote the fission of groups. We

predict that group size will be inversely correlated to the percentage of adult males in the group.

We developed a conceptual model examining intrinsic and extrinsic factors that influence the fusion or fission of groups in a small, free-ranging muskox population in northwest Alaska. We tested predictions concerning three major factors influencing group formation: habitat, foraging efficiency, and sociality. Although we lack data to test predictions regarding a fourth factor, predation, we used insights from the literature to include this variable in the model.

4.3 STUDY AREA

Cape Krusenstern National Monument is a 2,670 km^2 area adjacent to the coast of the Chukchi Sea in northwestern Alaska, USA (Fig. 4.1). Vegetation throughout the monument is Arctic coastal tundra. Beach ridges and extensive lagoons characterize areas near the coast, whereas further inland there are several groups of hills (up to 613 m in elevation) separated by wide expanses of gently rolling tussock tundra. The hills are used as wintering areas by muskoxen. Hilltops are generally barren and windswept, but the slopes are typically covered with *Dryas* heath and hummock tundra. Winters are long (the time from first snow to green-up exceeds 7 months), with frequent and severe windstorms. Annual average temperature in Kotzebue (ca. 50 km south-east of Cape Krusenstern National Monument), is -5.8 C and annual average precipitation is 22.5 cm, of which 12 cm falls between July and September. The lowest average minimum

temperature is -24.4 C (February) and the highest average maximum temperature is 15.1 C in July.

Muskoxen were reestablished in northwestern Alaska after extirpation in the late 1800s (Coady and Hinman 1984). In 1970 and 1977, 36 and 34 muskoxen, respectively, were released near Cape Thompson in northwestern Alaska. After growing slowly for the first 2 decades, the population began to increase steadily in the early 1990s. The population subsequently spread south to include Cape Krusenstern National Monument and stabilized at ca. 350-400 animals (Dau 2005).

During winter and spring, several thousand animals of the Western Arctic caribou herd (*Rangifer tarandus*), forming groups of up to several hundred animals, also reside in or move through Cape Krusenstern National Monument. Grizzly bears (*Ursus arctos*) are active in the area in summer, and wolves (*Canis lupus*) are present year-round. While we observed wolf predation on caribou during winter, the extent of predation by wolves or bears on muskoxen is unknown.

4.4 METHODS

We observed muskoxen in two seasons: summer (11 June through 9 July, 2002) and late summer/rut (15 July through 22 September, 2002). We also conducted a sex/age composition count in late winter (April 2002). Although mating generally does not commence until mid-August, we observed intense courtship and competitive behavior by males as early as 15 July. For this reason, we grouped data from the second half of July with the rutting period.

During summer 2002, we sampled in 2 periods, 11 June through 21 June, and 5 July through 9 July. We observed 24 groups during 13 continuous observation periods lasting from 15 to 525 minutes and conducted 288 group scans during activity bouts of muskox groups (Altmann 1974). During some observation periods, we could observe more than one group simultaneously. We observed an additional group in sex-age composition counts, but did not record behavior due to time constraints. We sampled the rutting period in 4 periods: 15 July through 23 July, 5 August through 13 August, 24 August through 3 September, and 16 September through 22 September 2002. We observed 14 groups during 21 continuous observation periods lasting from 75 to 660 minutes and conducted 469 scans during activity bouts of muskox groups. We included an additional two groups in sex-age composition counts, but did not observe them due to time constraints.

During summer and rut, we initially located muskox groups from fixed-wing airplanes at the beginning of each sampling period. We then selected a location for our base camp and from there approached muskox groups on foot. We observed animals through a 20-60 x spotting scope and 8 x 40 binoculars from distances of 100 - 1500 m. We defined a social group as any number of animals that traveled together and synchronized their activities at the time we began observing them. We only observed female-dominated groups containing adult females, young, and occasionally males. Groups were considered distinct from each other as long as they were not interacting or traveling together. When two groups moved into separate directions after splitting up, they were considered distinct from each other. Each group was observed as long as

visibility, weather, daylight, and observer stamina allowed. On two occasions, we interrupted observation bouts when animals moved towards us and became aware of our presence. During June and July, observation hours included the 24-hour cycle, but with most observations between 10 am and midnight. During all other times, observations were restricted to daylight hours.

We conducted group scan samples (Altmann 1974) at intervals of 15 minutes. During each scan we recorded: date, time, habitat, group size, overall group spread (greatest distance between peripheral animals on opposite side of the group) in m, and sex and age class, activity and distance to nearest neighbor of each individual herd member. Muskoxen were aged and sexed on the basis of horn development, body size, and coat length. We classified calves, yearlings, adult females ($\geq$ 2 years), 2-year old males, and adult males (>2 years old). We placed 2-year old males in a separate category because while not reproductive, they remained within mixed herds even during rut, indicating that their status in the group differed from that of non-reproductive adult males, who were competitively excluded from harem groups by the dominant herd bull. Two year old females in the study area were seen nursing calves on several occasions and were therefore grouped with adult females.

Muskox activities were classified as feeding (standing or moving slowly with head down, or visibly ingesting vegetation), walking (walking with head up), running (cantering or galloping), standing (stationary with head up), lying (resting in a sternal position or with whole body on the ground), playing (solitary or in groups; usually head-butting or running), agonistic (butting, displacing, chasing), scratching (standing

while rubbing against a stationary object), nursing (calves and females only; suckling or standing to let calf suckle) and sexual (courtship or mating behavior) (Oakes et al. 1992).

We identified 4 bounded and 2 unbounded habitat types used by muskoxen: unbounded habitats were barren (upland, barren or sparsely vegetated), *Dryas* (upland areas and upper slopes, partially vegetated), hummocks (upper or lower slopes), and tussock (low rolling slopes between hill groups). Bounded habitats were willow (thickets along creek banks and small drainages) and sedge (low lying wet meadows). Barren habitats were used by muskox groups only during resting bouts, while all other habitats were used for feeding and resting.

To characterize vegetation cover of the six habitat types, we selected two areas representative of each habitat type during summer 2002 and in each area sampled vegetation cover of 10 randomly placed 0.25m^2 quadrats. In each quadrat, 16 pin hits on vegetation were recorded according to the point-intercept method (Floyd and Anderson 1987).

4.41 Data treatment and statistical analyses

We derived percentage cover of major forage classes at the six habitat types from point-frame data by averaging the percentage of pin hits in each quadrant for each forage class (Floyd and Anderson 1987). In April 2002, we classified muskoxen according to sex and age after we located groups from a fixed-wing airplane and accessed them later by helicopter. During summer and rut 2002, we averaged group

sizes by season from groups observed during 11 June through 9 July (summer) and from 15 July through 22 September (rut). Repeated observations of the same animals were unavoidable because the study population numbered only approximately 150 animals. During summer and rut, muskox groups were transient and repeatedly broke apart and reformed into new groups. Any newly formed group was considered a unique group and was observed separately, even if it contained some of the same individuals as previously observed groups. Recognizable individuals were seen in as few as 1 and as many as 5 different groups. Repeated observations on the same animals in different groups were unavoidable. However, because our sampling unit was the group, and our goal was to characterize behavior of individuals within a particular group context, this did not affect our analyses.

We defined group forage efficiency as the percentage of active animals that were feeding (Berger 1978). We determined this measure of forage efficiency in four habitat types used most often by muskoxen: willow, sedge, *Dryas*, and hummock. For analyses of foraging efficiency in each habitat, we combined all scans from an observational period of a given group in a given habitat into one data point.

We averaged the percentage of group scans in each habitat type for each of the six sampling periods and used linear regression to test for seasonal change in habitat use. We used linear regression to test the relationship between individual spacing and group size, between habitat use and group size, between percentage of males and group size, and between group foraging efficiency and group size in the four most frequently used habitat types (willow, sedge, *Dryas* and hummock). We used one-way analysis of

variance to test sex-age differences in individual spacing, differences in percent cover of forage classes between habitat types, differences in feeding efficiency between sex-age classes, and seasonal differences in group size. We used two-tailed t-tests to determine seasonal differences in sex-age composition and seasonal differences in feeding efficiency for each sex-age class. Probability values ≤ 0.05 were considered to be statistically different. All analyses were conducted with SYSTAT 10.2 (SPSS Inc., Chicago, Illinois).

4.5 RESULTS

4.51 Abundance, demographics and group size

We counted 163 muskoxen in Cape Krusenstern National Monument in April 2002. Mixed-sex herds were largest in late winter, intermediate during summer, and smallest during the rut, ($F_{2,46} = 7.9$, $p < 0.001$, ANOVA) (Table 4.1). The composition of mixed-sex herds also changed seasonally; the percentage of adult males was lower during summer than during rut ($t = -6.8$, df = 29, $p < 0.001$), while there was a trend for the percentage of two-year old males to increase towards rut ($t = -1.8$, df = 38, $p = 0.08$) (Table 4.1).

4.52 Habitat use

All vegetation classes (graminoid, moss, lichen, *Dryas*, shrub, forb [non-woody flowering plants and *Equisetum* spp.] and unvegetated [litter and bare ground]) differed

among habitat types ($F_{6,127} = 10.9$, $p < 0.0001$) (Table 4.2). Between June and September 2002, muskox herds underwent a shift in habitat use from unbounded upland *Dryas* ($F_{1,4} = 13.8$, $r^2 = 0.77$, $p = 0.02$) and hummock ($F_{1,4} = 15.2$, $r^2 = 0.79$, $p = 0.02$) habitats to bounded, lower elevation sedge meadows ($F_{1,4} = 11.2$, $r^2 = 0.74$, $p = 0.03$). Muskoxen used willow drainages consistently during July and August, but abandoned them as soon as willow leaves began to senesce in late August. Nevertheless, seasonal changes in the use of willow ($F_{1,4} = 0.81$, $r^2 = 0.17$, $p = 0.42$) and barren habitats ($F_{1,4} = 0.21$, $r^2 = 0.05$, $p = 0.67$) were not significant. Seasonal change in the use of tussocks approached significance ($F_{1,4} = 6.6$, $r^2 = 0.62$, $p = 0.06$) (Fig. 4.2).

During summer, larger groups used bounded willow habitat more often than smaller groups ($F_{1,22} = 13.85$, $r^2 = 0.39$, $p = 0.001$), but during rut, when group sizes were small, habitat use was unrelated to group size ($F_{1,14} = 0.25$, $r^2 = 0.02$, $p = 0.62$) (Fig. 4.4a).

4.53 Foraging efficiency

Group foraging efficiency did not differ between summer and rut for adult males (summer: 61.1 ± 4.4%, rut: 61.3 ± 5.9% (mean ± SE), $t = -0.02$, df = 14, $p = 0.98$), adult females (summer: 69.1 ± 3.1%; rut: 75.0 ± 3.1%, $t = -1.35$, df = 31, $p = 0.19$), and 2-year old males (summer: 68.0 ± 5.3%; rut: 72.3 ± 5.5%, $t = -0.56$, df = 24, $p = 0.58$), and was marginally significant for young animals (calves and yearlings combined; summer: 53.4 ± 4.0%; rut: 64.6 ± 3.7%, $t = -2.07$, df = 39, $p = 0.045$).

Because group foraging efficiency for all sex-age classes combined did not differ between seasons (summer: 61.4 ± 2.9%; rut 68.9 ± 3.4%, t = -1.67, df = 54, p = 0.10), we combined seasons for foraging efficiency analyses in individual habitats. Group foraging efficiency was unrelated to group size in spatially bounded sedge ($F_{1,6}$ = 0.02, r^2 = 0.003, p = 0.90) and willow ($F_{1,9}$ = 0.26, r^2 = 0.03, p = 0.62) habitats, but correlated negatively with group size in unbounded upland *Dryas* ($F_{1,15}$ = 5.36, r^2 = 0.26, p = 0.033) and hummock ($F_{1,18}$ = 6.92, r^2 = 0.28, p = 0.017) habitat types (Fig. 4.3). A decrease in foraging time was accompanied by an increase in the amount of active time animals spent standing (6.9% summer, 14.4% rut), walking (21.0% summer, 14.3% rut), or running (2.8% summer, 1.6% rut). Aggressive interactions comprised only 0.3% and 0.9% of all observations during summer and rut, respectively.

4.54 Sociality

Average individual spacing between group members decreased with group size during summer, when muskoxen fed primarily in unbounded habitats ($F_{1,37}$= 8.18, r^2 = 0.18, p = 0.007), but not during rut, when they fed in bounded habitats ($F_{1,32}$= 0.08, r^2 = 0.003, p = 0.78) (Fig. 4.4b). Adult males maintained a greater distance to their group neighbors than other sex-age classes. Individual spacing scaled to increasing body size of sex-age classes ($F_{4,4193}$ = 152.4, p < 0.0001, Fig. 4.5). The percentage of adult males in the group was unrelated to group size in summer ($F_{1,23}$ = 0.20, r^2 = 0.009, p = 0.66) and approached significance during rut ($F_{1,14}$ = 4.28, r^2 = 0.23, p = 0.06). We

summarize the complexities of muskox group formation in a conceptual model (Fig. 4.6).

4.6 DISCUSSION

The effect of habitat on group sizes is difficult to interpret because both habitat use and group sizes also differed seasonally. Nonetheless, when we adjusted for season, we detected no effect of habitat on group size during rut. We therefore reject our prediction that when feeding in unbounded habitats, muskox group size should be larger than when using bounded habitats.

We reject the hypotheses that group foraging efficiency increases with group size in unbounded habitats but decreases with group size in bounded habitats. Instead, we observed an inverse relationship between foraging efficiency and group size in unbounded habitats and no relationship in bounded habitats. During rut, however, when muskoxen fed primarily in bounded habitats, group sizes may not have been large enough to affect foraging efficiency. To our knowledge, ours is only the second study that detected a negative relationship between group size and foraging efficiency in ungulates (see Molvar and Bowyer 1994).

Our hypothesis that adult males maintain less cohesion to group members than other sex-age classes was supported because adult males were separated by the largest distance to their neighbors of any sex-age class. However, we reject the hypothesis that group size is inversely correlated to the percentage of adult males in the group. We

observed no such relationship in summer, while the relationship approached significance during rut.

In accordance with most researchers studying seasonal changes in muskox group size (Tener 1965, Reynolds 1993), we observed larger groups in winter than during other seasons. Cote et al. (1997) noted such an increase only for bachelor bull groups, but not for mixed-sex groups on Victoria Island, Canada. Our mean winter, summer, and rut group sizes of 23, 19 and 11 are similar to those reported by Reynolds (1993) for northeastern Alaska. A summary of muskox group sizes (Heard 1992) shows considerable variation among Arctic regions, indicating that selective pressures influencing group size differ regionally. Nevertheless, Heard (1992) concluded that muskox group size was positively correlated to wolf density and was unrelated to social factors.

4.61 Conceptual model: effect of habitat

Arctic herbivores maximize foraging opportunities by following the gradient of plant phenology throughout the growing season (White 1983). Many researchers have noted a seasonal shift in habitat and diet selection (Parker 1978, Oakes et al. 1992, Forchhammer 1995), which reflects changing requirements for protein and energy (Forchhammer and Boomsma 1995) and variations in phenology among plant growth forms and tissues. Similarly, muskoxen in Cape Krusenstern National Monument shifted habitat use from forb-rich habitats in early summer, such as *Dryas* and hummock, towards sedge meadows during rut. Willow thickets were used consistently

during summer but were abandoned as soon as leaves senesced in late August. Oakes et al. (1992) also observed a late summer shift towards more graminoid-based habitats on Banks Island, Canada, as did Thing et al. (1987) in northeast Greenland. In Cape Krusenstern National Monument, the shift towards higher use of sedge habitats during rut constitutes a reduction in feeding patch sizes. Nevertheless, in contrast to our expectation that smaller patches would favor smaller groups, group sizes within season were mostly unrelated to habitat use.

In Cape Krusenstern National Monument, muskoxen tend to remain in coastal sedge habitats until snow accumulation in mid – to late winter forces them to seek out upland wintering areas. Groups then aggregate on the relatively few available winter habitats (Ihl, in preparation). Several researchers have noted a correlation between animal densities and group sizes, suggesting that when habitats are bounded, ungulates may aggregate in larger groups than would be optimal. Raman (1997) suggested that increases in group size of axis deer (*Axis axis*) resulted from a two-step process: first, the aggregation of groups in newly attractive habitats after rainfall, and second, the fusion of groups because of their high encounter rate. We suggest that a similar process is responsible for the large group sizes of muskoxen on winter ranges.

4.62 Conceptual model: effect of foraging

In cervids (Raman 1997, Bowyer et al. 2001, Bowyer and Kie 2004), foraging efficiency is generally positively correlated with group size. An increase in group size could benefit foraging efficiency because individuals in larger groups are less

vulnerable to predation and have to allocate less time to vigilance (Underwood 1982, Bowyer et al. 2001, Fortin et al. 2004). Nevertheless, this outcome could be expected to be true only as long as feeding patches are extensive enough to accommodate large groups without added feeding competition (Monaghan and Metcalfe 1985). If food sources or patch sizes are limiting, foraging efficiency in large groups would be expected to decrease because of increased competition and aggressive interactions among group members (Watts 1985). In northeast Greenland, muskoxen responded to a high synchrony in the growth of *Salix arctica*, which likely shortened the time muskoxen could access growing willows, by spatially dispersing and reducing group size (Forchhammer at al. 2005).

In Cape Krusenstern National Monument, foraging efficiency and individual spacing declined with increasing group size in spatially unbounded *Dryas* and hummock habitats. Muskoxen differ from cervids in their predator defense strategy: they rely on coordinated group defense rather than flight (Gray 1987). To maintain coherence for effective group defense, muskoxen may have to stay within a certain distance to their neighbors. This limits the area over which a group can spread, even in spatially unbounded habitats, and in theory pre-determines the largest possible spread for a given group. If resources are limited or sparsely distributed within such a spread, as is the case in partially vegetated *Dryas* and hummock habitats, it is possible that feeding competition ensues between herd members. Additionally, a higher encounter rate between animals in a larger group may result in a higher rate of social interactions, which reduces foraging efficiency. This latter effect, however, should be independent of

habitat type. Molvar and Bowyer (1994) also reported an inverse relationship between group size and foraging efficiency for Alaskan moose, which have only recently evolved sociality: larger groups resulted in more aggression between group members, which limited opportunities for foraging. In contrast, we observed aggressive interactions between muskoxen only 0.3% and 0.9% of the time during summer and rut, respectively. This is comparable to the low rate of aggressive interactions other researchers have observed in social ungulates during foraging (Fortin et al. 2004). Unlike moose, muskoxen and other highly social species have evolved subtle communication signals among group members. Displacement of foraging neighbors may therefore rarely involve overt aggression, but rather be expressed in an increase of time spent standing or walking as animals observe and move to avoid each other.

4.63 Conceptual model: effect of sociality

Individual spacing of group members scales to body size (Fig. 5), with adult males keeping the largest distance to their neighbors and thereby contributing the least to group cohesion. During summer, males spend time and energy seeking out potential mates by moving long distances and moving in and out of groups. The larger distances between adult males may also reflect competitive social relationships between them.

Muskox groups tend to be smallest during rut, when the competitive behavior of adult males presumably contributes to the break-up of larger groups (Smith 1976, Reynolds 1993). This outcome is in contrast to many cervid species, which tend to aggregate in larger groups during rut (Raman 1997). If the presence of more than one

male per group increases group tendency to break up, then group sizes should be inversely correlated to the percentage of adult males. We observed no such relationship in summer, but during rut, when males are more active in controlling the movements of females (Ihl and Bowyer, *in review*), the inverse relationship between group size and percentage of adult males approached significance. In Greenland, an increase of females in the population resulted in larger groups (Forchhammer et al. 2005). Sizes and male-female ratios during the rut may also be limited by the number of females a single breeding bull can control. It is likely that the smaller group sizes during the rutting season in Cape Krusenstern National Monument are due to the combined effect of the fracturing influence of rutting males and the simultaneous need of groups to feed in sedge habitats, which occur in smaller patches.

We observed that whenever two muskox groups meet, there appears to be an attraction between them that invariably leads to the fusion of groups (Ihl and Bowyer, *in review*). This effect may be more pronounced in areas of high density, where encounter rates between groups are higher (Caughley 1977). Muskox groups are led by adult females, which may initiate movements towards neighboring groups. Decisions by group leaders may also contribute to group fusion. Conversely, conflicts in leadership decisions between female members of the same group may lead to group fission (Ihl and Bowyer, *in review*).

4.64 Conceptual model: effect of predation

The effect of predation on group formation in our study population is difficult to ascertain, because we observed no predation events and the extent of predation on muskoxen in the study area is unknown. Reynolds et al. (2002) report that grizzly bears frequently prey on muskoxen in northeastern Alaska. Wolves aggregate in packs during winter, and wolf attacks on muskoxen typically involve packs, not individual wolves (Mech 2007). A higher predation risk from wolves may therefore contribute to the need to form larger groups in winter (Heard 1992). We observed that the characteristic defensive circle formation of muskoxen was triggered by approaching humans or circling airplanes. This outcome indicates that predator defense behavior is an intrinsic characteristic of muskox behavior, which persists even in areas of very low or absent predation pressure.

Vigilance behavior, which may influence group sizes through its effect on foraging efficiency (Fortin et al. 2004), might be of less importance to muskoxen than other prey species. Early predator detection may be more important in species whose predator defense relies on flight than in species that practice group defense. Caribou, which live in similar habitats and have similar predators, rely on flight and consequently practice vigilance behavior to a higher degree than muskoxen (Roby 1978, Boving 1994).

The tightly coordinated predator defense of muskoxen relies on an implosion of the group towards its center (Mech 1988, Mech 2007), which requires that individuals maintain proximity to their neighbors. The formation of defensive circles may be

inefficient or take longer in very large groups, exposing individuals to predation risk. We suggest that in muskoxen, the need for coordinated group defense puts an upper limit on the size and spread of muskox groups even in wide-open habitats.

4.65 Decisions by individuals based on physiological state

Because groups are composed of individuals, it is necessary to consider how the seasonal physiological state of individuals may influence their tendency to form larger or smaller groups, or, in the case of adult males, leave or join mixed-sex groups. Outside of the rut, movements of adult males are likely driven by foraging requirements rather than reproductive needs. Because of their larger body size, adult males have a bulkier, more fibrous diet than females, requiring them to seek out more sedge-based habitats than female-dominated groups during summer (Barboza and Bowyer 2000). The presence of adult males in mixed-sex groups was consequently low during summer, and on several occasions we observed adult males joining or splitting from groups without disrupting cohesion among remaining group members. Adult males are the only sex-age class in muskoxen that is occasionally solitary. Nevertheless, even though their larger body size may make them less vulnerable to predation, they may join in bachelor groups to reduce predation risk (Gray 1987). Reproductive females have high protein requirements during lactation (White 1983). Consequently, female groups seek out habitats that offer protein-rich legumes and other forbs (Klein 1990) in early summer, such as upland hummocks, *Dryas*, and the understory of willow thickets. Larger group sizes in summer may also benefit females by reducing predation risk on young calves.

Two-year old males, which are non-reproductive, resemble adult females in body size. Their foraging requirements may therefore be closer to that of non-reproductive females than adult males, which may encourage them to remain with female groups during summer. Although we did observe several two-year old males in bachelor groups, their percentage in mixed-sex groups did not significantly differ between summer and rut.

4.66 Management implications

Managers of muskox populations must be aware of the importance of different habitats in different seasons, as well as the seasonal fluctuations in muskox sociality and group size. Surveys and censuses should optimally be conducted at more than one time per year to reflect these seasonal dynamics. Growing and expanding muskox populations need an abundance of habitats that offer protein-rich forage to growing animals and reproductive females, such as the *Dryas* and hummock habitats used by female groups during early summer. In areas with relatively high snow fall, where muskoxen are confined to small, low-quality ranges for many months during winter, habitats such as sedge meadows, which offer abundant and high quality forage during the period between plant senescence and snow accumulation allow muskoxen to maximize fat accumulation before winter.

Climate change may increase snow depth and willow abundance in the future (Tape et al. 2006). Increased snow may force muskoxen to aggregate in larger groups on smaller patches during winter. This may increase stress and foraging competition potentially resulting in reduced productivity. A higher abundance of willow thickets has

potential benefits for summer foraging: muskoxen may be able to use high-biomass willow habitats more frequently and form larger groups while they do so.

4.7 ACKNOWLEDGMENTS

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TABLE 4.1: Seasonal changes in sex-age composition and size of mixed-sex muskox groups in Cape Krusenstern National Monument in 2002. Numbers for sex-age classes are percentages of total group size with standard errors in parentheses. Sample sizes are numbers of groups observed. Late winter was excluded from statistical analyses of sex-age composition because it did not include a calf class.

Sex/age class	Late winter (n=6†)	Summer (n=16††)	rut (n=25††)
Adult male*	22.3 (4.8)	2.7 (0.9)	13.7 (1.3)
Adult female*	65.8 (6.2)	55.9 (2.5)	40.4 (2.1)
2-year old male	7.7 (2.3)	12.5 (2.4)	18.4 (2.3)
Yearling	4.1 (0.9)	2.1 (0.7)	1.5 (0.8)
Calf	0 (0)	26.9 (1.1)	26.0 (1.3)
Average group size**	23.0 (5.7)	19.0 (2.2)	10.8 (0.9)

* differs between summer and rut ($p < 0.0001$, two-tailed t-Test)
** differs between winter, summer and rut ($p < 0.001$, ANOVA)
† based on an aerial survey with ground-truthing of sex-age classes
†† based on ground surveys

TABLE 4.2: Percent vegetation cover at six major habitat types in Cape Krusenstern National Monument between June 11 and September 22, 2002. Means with standard errors in parentheses.

	Vegetation classes						
	graminoids	moss	lichen	*Dryas*	shrub	forb	unvegetated
Unbounded habitats							
Barren	0.9 (0.5)	0	3.5 (1.2)	2.2 (1.0)	0	0.3 (0.3)	93.1 (2.0)
Dryas	20.0 (3.6)	0.9 (0.7)	9.4 (1.9)	22.5 (2.5)	0	3.4 (1.0)	43.8 (4.3)
Hummock	43.9 (4.0)	15.2 (3.0)	2.2 (0.9)	4.7 (1.4)	11.8 (2.0)	13.5 (2.9)	8.7 (1.7)
Tussock	31.8 (2.9)	7.6 (1.3)	1.3 (0.6)	0	48.9 (2.7)	2.2 (0.8)	8.4 (1.5)
Bounded habitats							
Willow	27.8 (5.8)	4.4 (1.5)	0	0	50.6 (7.9)	14.7 (3.2)	2.5 (0.8)
willow understory*	32.1 (7.2)	8.5 (2.1)	0	0	0	51.3 (7.1)	8.0 (3.3)
Sedge	75.9 (4.2)	2.2 (0.9)	0.9 (0.5)	0	0.6 (0.6)	4.7 (2.0)	15.7 (3.0)

all cover classes differ significantly between habitat types at $p < 0.0001$, ANOVA, SYSTAT.

* same habitat as 'willow'; represents ground cover beneath willow bushes.

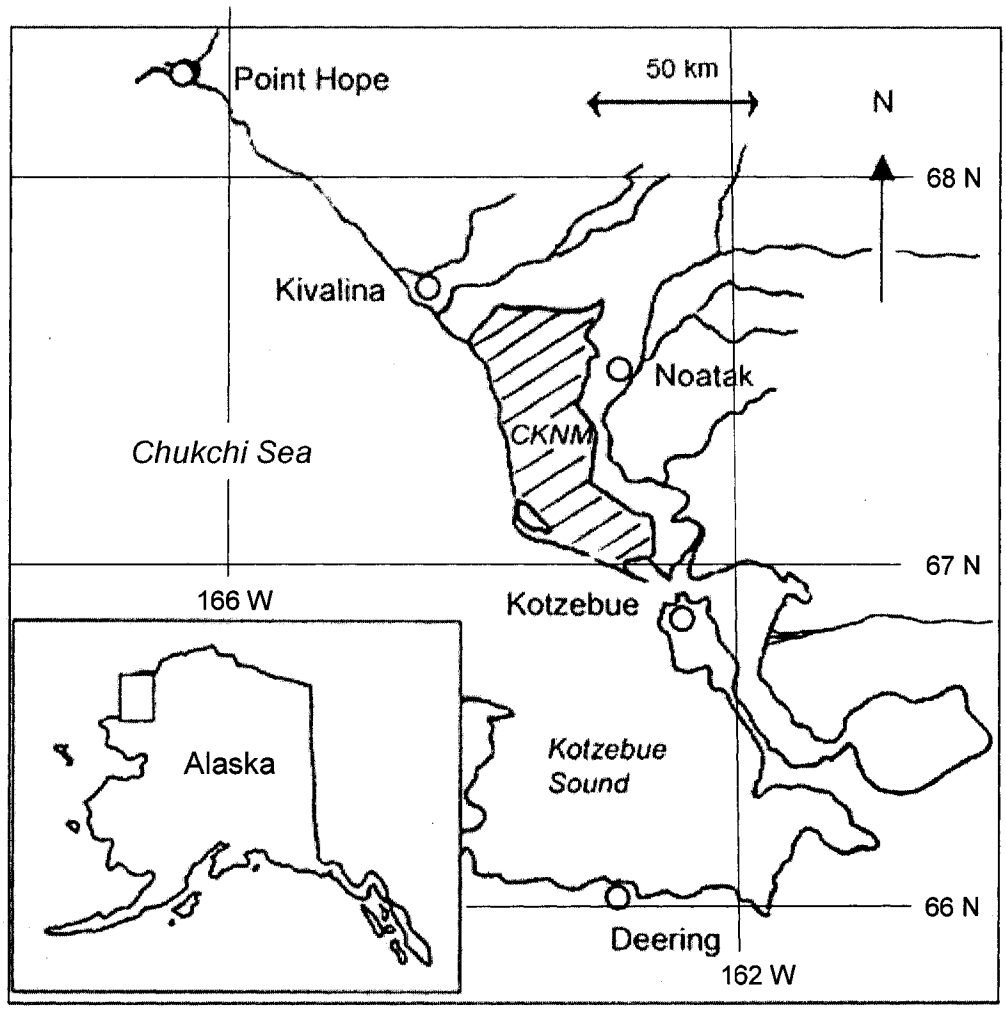

FIGURE 4.1: Location of Cape Krusenstern National Monument (CKNM) study area in northwestern Alaska.

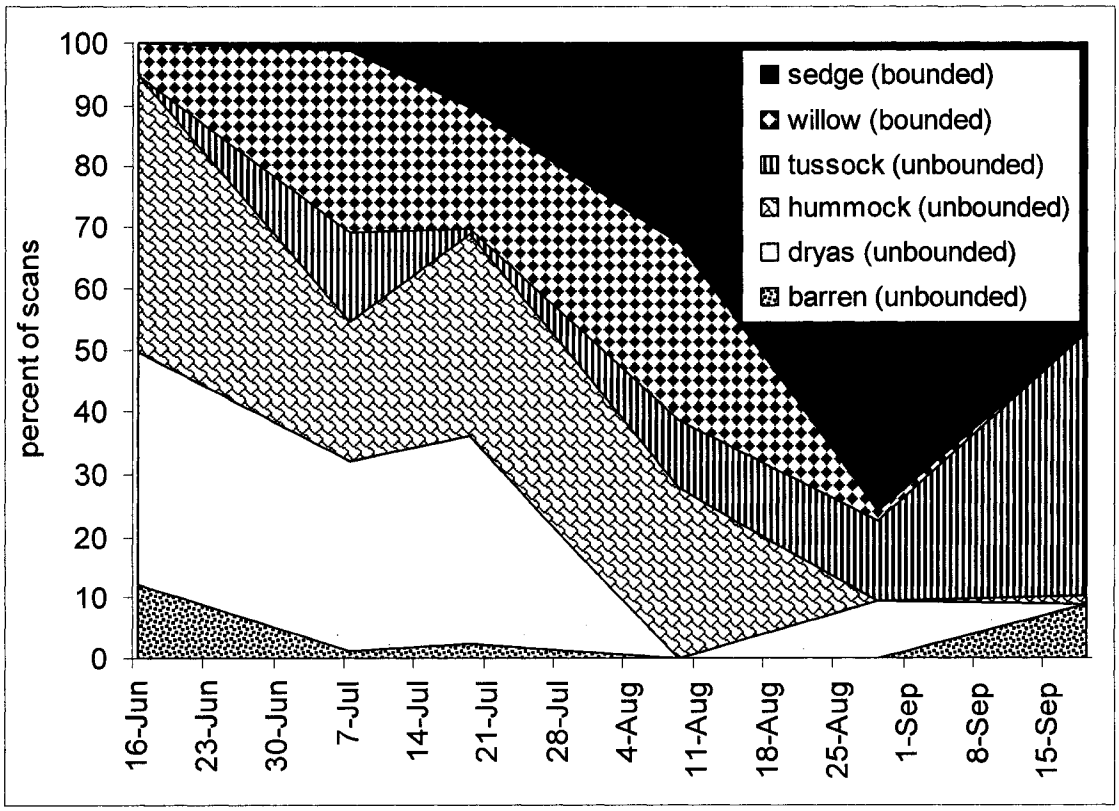

FIGURE 4.2: Use of spatially bounded and unbounded habitat types by mixed-sex muskox groups in Cape Krusenstern National Monument during June – September, 2002. For each of six sampling periods, the number of group scans in each habitat is expressed as a percentage of the total number of scans. Sampling periods and sample sizes (number of scans) were June 11-21, n=211; July 5-9, n=81; July 15-23, n=125; August 5-13, n=101; August 24 – September 3, n=177; September 16-22, n=57.

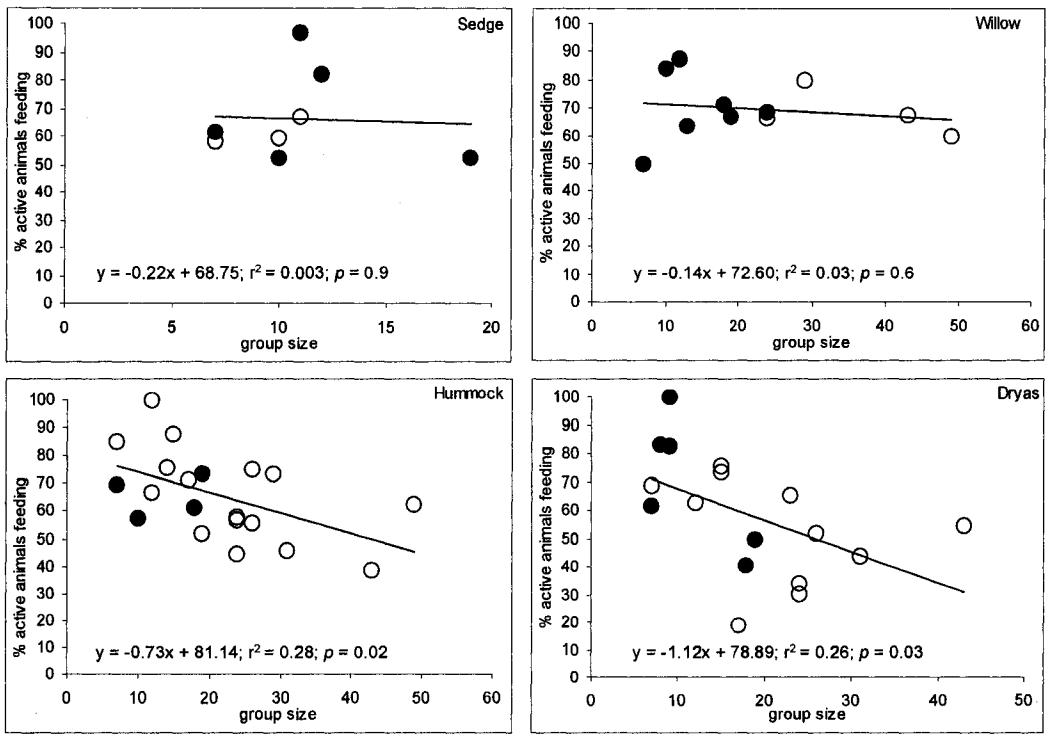

FIGURE 4.3: Foraging efficiency (percent of active animals feeding) in relation to group size of mixed-sex muskox groups in four habitat types in Cape Krusenstern National Monument during summer and rut 2002. Open circles: summer; closed circles: rut. Regressions were run on both seasons combined.

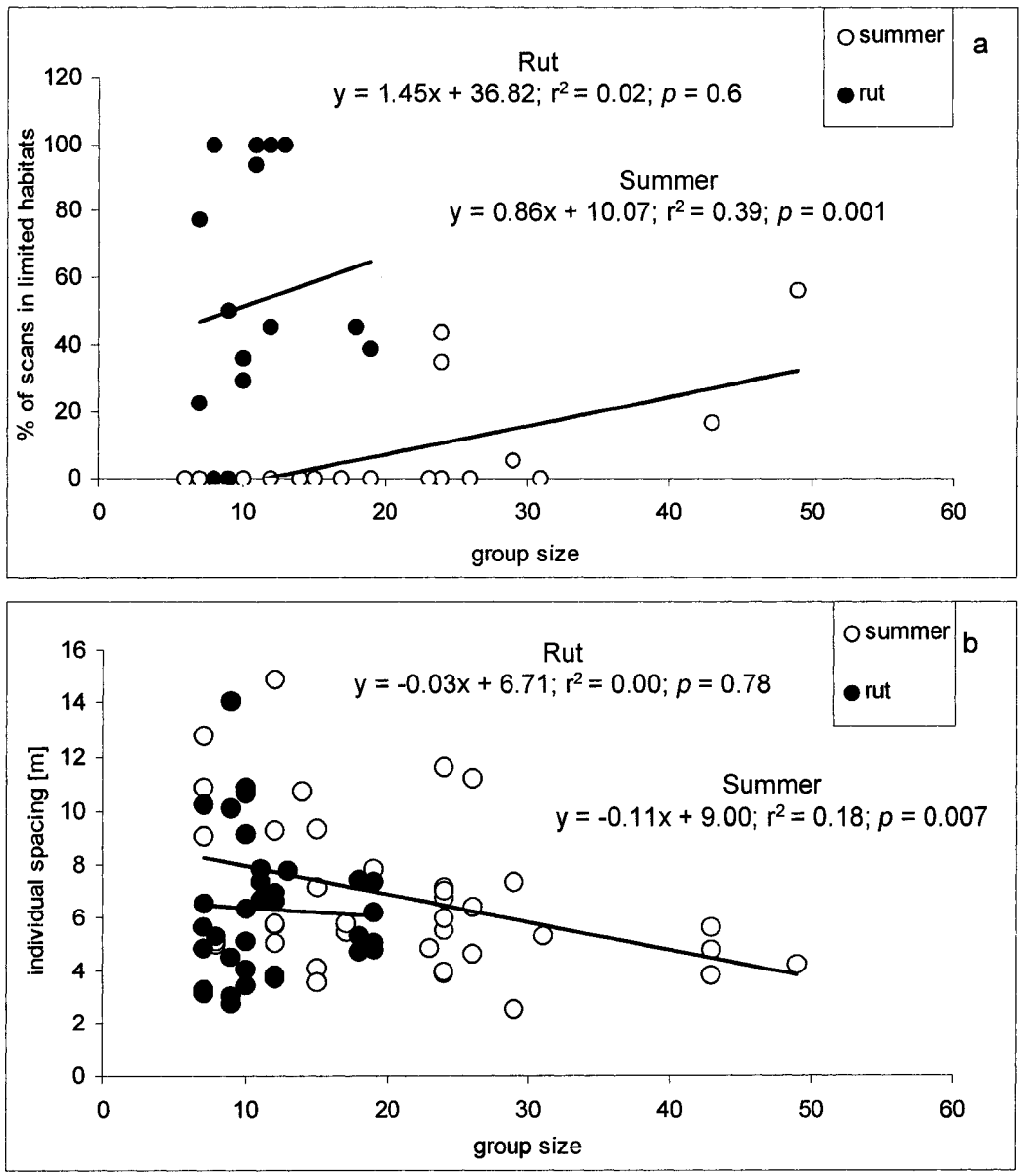

FIGURE 4.4: Relationship between habitat use (a) and individual spacing (b) versus group size of mixed-sex muskox groups in Cape Krusenstern National Monument during summer and rut, July-September, 2002.

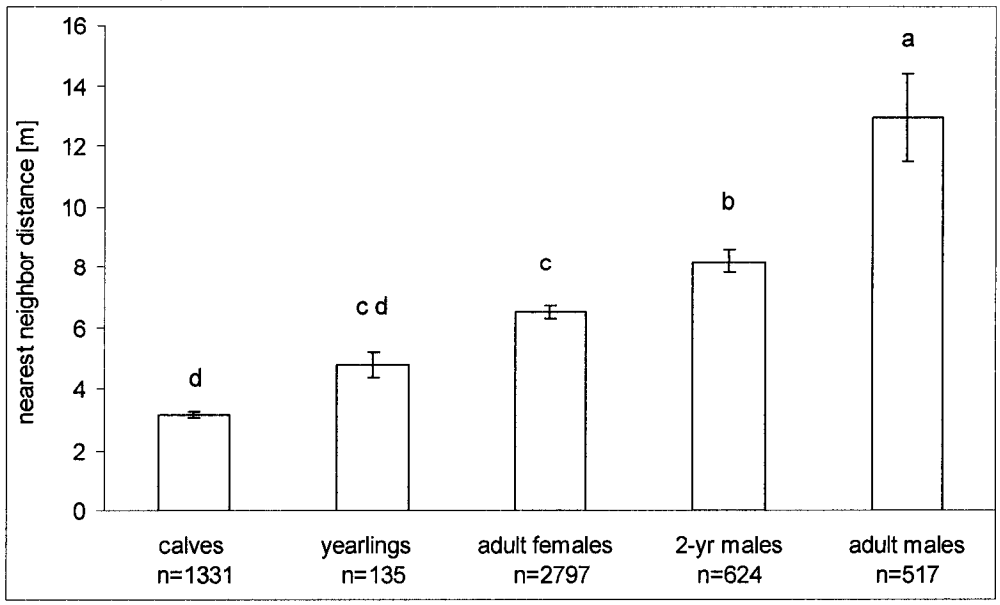

FIGURE 4.5: Nearest-neighbor distances across sex-age classes in mixed-sex muskox groups in Cape Krusenstern National Monument during July-September, 2002. Sample sizes are numbers of individual observations. Columns not sharing a letter are significantly different from each other (ANOVA, between columns b and a $p < 0.012$; all other $p < 0.0001$)

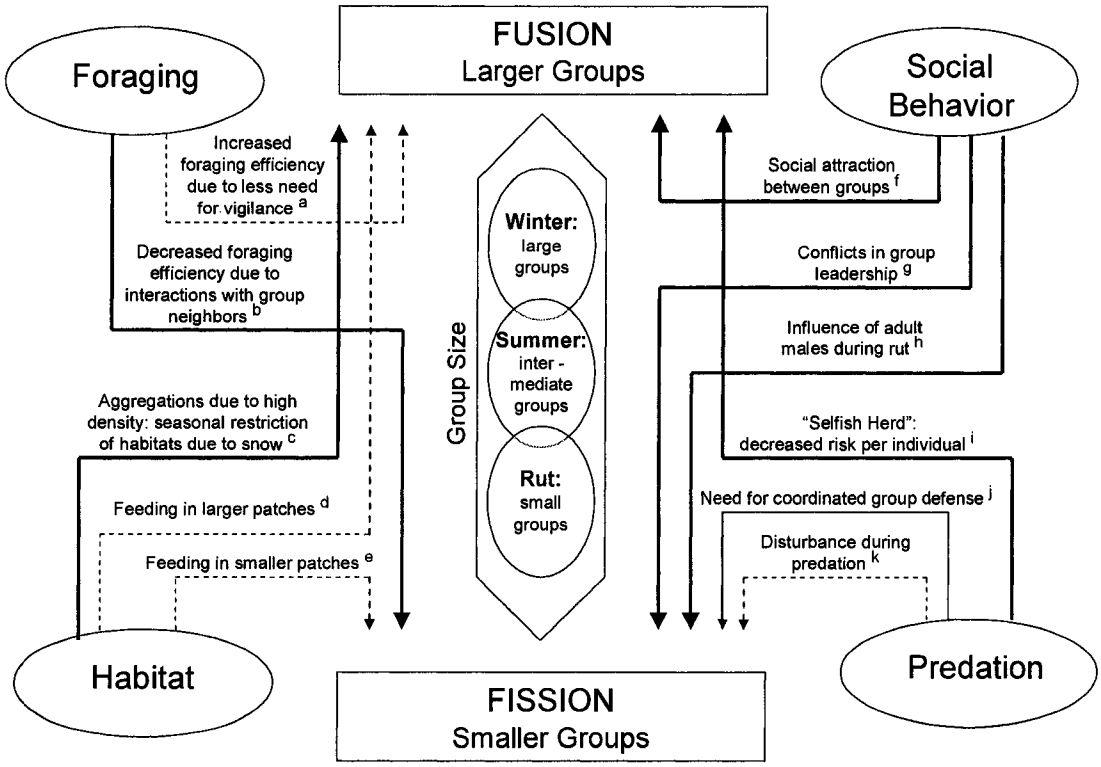

FIGURE 4.6: Conceptual model of factors influencing fission and fusion of mixed-sex muskox groups. Bold continuous lines with large arrow heads represent factors that have been observed in muskoxen. Thin continuous lines with small arrow heads represent factors that are hypothesized based on data in this study. Dashed lines represent factors that are hypothetical for muskoxen but have been confirmed in other group-living ungulates. References are: [a] Fortin et al. 2004; [b] Molvar and Bowyer 1994, this study; [c] Heard 1992, Ihl and Klein 2001; [d] Jarman 1974; [e] Jarman 1974; [f] Raman 1987, Ihl and Bowyer, in review; [g] Ihl and Bowyer, in review; [h] Gray 1987, Gunn 1992, Ihl and Bowyer, in review; [i] Hamilton 1971, Heard 1992; [j] hypothesized based on this study; [k] Reynolds et al. 2002, Reynolds, personal communication.

GENERAL CONCLUSIONS

The objective of this study was to gather information on sociality and winter foraging of muskoxen in Cape Krusenstern National Monument, Alaska. Chapter 1 concludes that moss is nearly indigestible by muskoxen and may even place animals in a negative energy and protein balance if it is eaten in large quantities. Chapter 2 examines moss consumption in an ecological context and concludes that muskoxen eat more moss on poor quality winter ranges where graminoids, their favored forage, are less available and snow is harder, resulting in a greater energetic cost of cratering. Muskoxen in Cape Krusenstern face larger local differences in winter range quality and potentially more moss consumption than muskoxen on the Seward Peninsula ca. 100km to the south, although they do not eat more moss overall. Most importantly, Cape Krusenstern muskoxen are more spatially confined on their winter ranges than Seward Peninsula muskoxen, and at the higher densities observed on Cape Krusenstern winter ranges, density related strongly to moss consumption (Chapter 2). The available area and quality of winter ranges in Cape Krusenstern appears more limiting than on the Seward Peninsula and may contribute to reducing carrying capacity in Cape Krusenstern. Consequently, it is unlikely that the Cape Krusenstern muskox population will increase in number in the future. Hunting quotas will therefore most likely have to remain small and on a subsistence basis only.

But should a hunt include bulls and cows, or bulls only? Chapter 3, which examines the respective roles of males and females in muskox society, may help answer this question. Because adult females are leaders of group movements during summer

(Chapter 3), it is likely that they are also responsible for the selection of winter ranges. But how do females select winter ranges? Other researchers and I have observed that the same group can winter in the same area in consecutive years, and many wintering areas are occupied by muskox groups for several consecutive years (Ihl and Klein 2001). Does tradition play a large role in selecting a winter range? Do females simply go to a familiar place, a range where they have wintered before? Once muskoxen are on their winter ranges, their reluctance to leave suggests that the initial choice of winter range is an important one. For these energy-conserving animals, who cannot afford great energy expenditure during winter, it may be a safer choice to go to a known winter range, even if it is not an optimal one, than taking the risk of setting out to a new place.

During summer, muskox groups are more mobile than in winter and frequently find each other to combine and eventually break up again in new configurations (Chapter 4). The removal of a leading female during this time would therefore be of little consequence. However, human hunting will most likely occur during the winter months. In this vast, remote region, hunters have to wait for enough snow to accumulate so that they can travel by snow machine. During winter, muskox groups are isolated from each other and are confined to their respective winter ranges. If a prominent member of the group is shot at this time, it will not be replaced until spring, when groups leave winter ranges and mingle again with other groups. On the other hand, there may in general be little need for group leaders during winter because there is little need for movement once muskoxen have reached winter ranges. However, my observation of the Sealing Point muskox group (Chapter 2), which trekked across a frozen lagoon in

late March 2001 to reach a new winter range with better forage availability, suggests that the experience and knowledge of group leaders can on occasion be vital even during winter, when a group is faced with a choice between potential starvation and energy-costly relocation.

Adult muskox males can spend winter alone, in small bachelor groups, or in mixed-sex groups (Gray 1987, Reynolds 1993). Those males who winter in mixed-sex groups typically split from these groups during calving and early summer, as evidenced by the very low percentage of males I observed in Cape Krusenstern in mixed-sex muskox groups during June. Hunting pressure on mixed-sex groups in late winter can stress groups and force them to leave winter ranges at a time when the energetic cost for such a move is high. For this reason, it may be inadvisable to hunt females or males in mixed-sex groups during winter. Hunting should include males only, and hunters should be encouraged to focus on bulls that are single or in bachelor groups. This, however, raises questions of whether the hunting of only one sex and age class will skew the demographic composition of the population in the future, and whether these hunted males will be sufficiently replaced by either recruitment or immigration.

My study raises a number of additional important questions regarding muskoxen ecology. For example, it is unclear to which extent the Cape Krusenstern muskoxen interact with other muskoxen to the south and north. Movements of muskoxen in and out of Cape Krusenstern may be more restricted towards the east, where the Noatak valley and the western Brooks Range form natural barriers, and where there are no established muskox populations. During my field research in Cape Krusenstern and on

the Seward Peninsula I have observed that young bulls are expelled from mixed-sex groups by the dominant rutting bull during their fourth summer, when their horn boss has begun to develop. These three-year old bulls, as well as single mature bulls, often roam long distances during summer in search of breeding opportunities (Smith 1989). The question of whether bulls disperse out of or into Cape Krusenstern is important because if a hunt targets adult males only, but these are not replaced by immigrating males, the demography of the population could shift in favor of females, which could affect group structure and reproductive rates (see Gunn 1992). Because of the remoteness of the study area, questions of dispersal can likely only be answered in a study that employs radio or satellite telemetry.

My final chapter unites the complexities of foraging behavior, habitat restrictions, and social behavior into a conceptual model that interprets decisions of muskoxen regarding group formation: when to fuse, when to split up, whether to be in larger or smaller groups during different seasons (Chapter 4). Such a model, though helpful in pointing out the main selection pressures driving group formation, can only approximate the real complexities of muskox social life. Every hour spent watching wild animals will tell a careful observer that animals are motivated and influenced in far more subtle ways than the relatively crude behavioral categories we record. I discovered that conducting a study of social behavior on free-ranging animals is rather like watching several hundred hours of soap operas, and then trying to summarize who-did-what-to-whom in a spreadsheet. Naturally, one has to simplify and summarize complex, subtle behaviors into broad categories, such as "leading", "following" or

"manipulating". This difficulty may be one reason why studies of free-ranging animals under natural conditions are the least common category of behavioral studies (but see Prins 1996, McComb et al. 2001). The field of animal behavior relies heavily on the experimental approach which places captive animals into a simplified environment where variables can be controlled (for example, Reebs 2000). Nevertheless, the difficulty of quantifying complex social behaviors should not deter researchers from studying free-ranging animals, since the ultimate test of findings obtained in the lab or through computer modeling is whether they will hold up in the far more intricate real world that animals inhabit.

There may be future changes in Cape Krusenstern that could affect the biology of muskoxen there. Global warming could bring changes in vegetation and snowfall. A widespread increase of shrubs has been observed throughout tundra habitats in Alaska (Tape et al. 2006), and this could reduce graminoid availability for muskoxen in the future. Another likely global warming scenario is increased winter snowfall (Heggberger et al. 2002), which may further reduce available winter ranges for muskoxen and lead to a decrease in population size. Warmer winter weather may also bring an increase of freeze-thaw cycles in early winter, which can deposit a hard layer of ice on the vegetation which is nearly impenetrable to foraging Arctic ungulates and can lead to widespread starvation (Reimers 1983).

Environmental changes may trigger changes in animal populations. Although Cape Krusenstern lies outside the main wintering areas for the Western Arctic caribou herd, a further increase of numbers in that herd may bring more wintering caribou to

Cape Krusenstern in the future. Conversely, caribou could cease to winter there if their numbers decline. Wintering caribou will likely bring wolves (*Canis lupus*) to the area, which, especially after a decline in caribou numbers, may increase predation on muskoxen. Bear (*Ursus arctos*) numbers may also change, or bears could prey more actively on muskoxen, as happened in the Arctic National Wildlife Refuge in northeastern Alaska, where an increase in bear predation (Reynolds et al. 2002) may have contributed to the decline of that population. Because muskox numbers in Cape Krusenstern are low (approximately 150-200 animals), the population is likely vulnerable to any adverse changes. Managers should monitor population numbers yearly and be alert to any sudden declines in numbers.

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